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Some Cretaceous and Palaeogene *Trinacria* (diatom) species

Patricia A. Sims and Robert Ross

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Patricia A. Sims and Robert Ross

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Synopsis

Descriptions are given of those species of *Trinacria* Heiberg that have buttresses at the base of the labiate processes, these buttresses sometimes extended over the valve face and united to form external costae. There are ten species, two of them divided into two formae, with this characteristic. Full synonymies are provided and the misidentifications in the literature are pointed out. Four of the species were originally placed in the genus *Triceratium* Ehrenberg and have not previously been transferred to *Trinacria*. The following new combinations are made: *Trinacria cornuta* (Grev.) P. A. Sims & R. Ross, *T. cancellata* (Grev.) P. A. Sims & R. Ross, *T. senta* (Witt) P. A. Sims & R. Ross, and *T. caudata* (Witt) P. A. Sims & R. Ross. The following new taxa are described: *T. cornuta* forma *pentagona* P. A. Sims & R. Ross, *T. ecostata* P. A. Sims & R. Ross, *T. fimbriata* P. A. Sims & R. Ross, *T. barronii* P. A. Sims & R. Ross, and *T. barronii* forma *tetragona* P. A. Sims & R. Ross. *Trinacria* belongs to the subfamily Hemiauloideae of the Biddulphiaceae. The content of this subfamily is discussed. The earliest records of five of the species are from the upper Cretaceous. Of these, *Trinacria interlineata* J. A. Long et al. certainly, and *T. barronii* probably, extended into the lower Palaeocene, whilst *T. cancellata* and *T. senta* persisted until the Oligocene, the latter possibly also into the lower Miocene. Two species, *T. caudata* and *T. coronata* Witt, first recorded from the Palaeocene, survived until the upper Miocene.

Introduction

In our latest paper (Ross & Sims, 1987) we re-established the genus *Solium* Heiberg, distinguishing it from *Trinacria* principally because it has interlocking linking spines and a subocellus on each elevation. In the course of preparing that paper we had occasion to investigate *Solium princeps* M. Peragallo, which we found to be a synonym of *Trinacria cristata* Gombos. We also examined the type specimen of *T. excavata* forma *tetragona* A. Schmidt, which proved to be very

closely related to *T. cristata* but not at all closely to *T. excavata*. At the time we regarded *T. cristata* and *T. excavata* forma *tetragona* as conspecific, but we now consider them separate species. *Triceratium cornutum* Grev. and *T. acutangulum* Grev. are earlier names for the species to which *Trinacria excavata* forma *tetragona* belongs. Specimens in the collections of the British Museum (Natural History) of a closely related but undescribed species from the Palaeocene of middle Volga basin had been identified as *T. excavata* forma *tetragona*.

These three quadripolar species all possess labiate processes with buttresses at the base of their external tubes. We have accordingly examined all the tripolar species of *Trinacria* with buttressed labiate processes, including those with more than one labiate process in which the buttresses merge to form a pattern of external costae on the valve face. None of these, however, proved to be tripolar forms of the quadripolar species we had examined, although we did find one undescribed species with tripolar and quadripolar forms. Some of the tripolar species had originally been described as species of *Triceratium* and had never been transferred to *Trinacria*; the identity of the species to which some of the earlier published names applied had not been realized; in more recent literature there was evidence of mis-identifications and misapplications of names. For these reasons synonymies and descriptions are given below for all the species of *Trinacria* with buttressed labiate processes.

Sources of specimens and records

Because of the extent to which specimens of the species with which we deal in this paper have been misidentified, we have included in the distribution data for each species only those records based on specimens that we have seen and those accompanied by illustrations, with a very few exceptions discussed under the individual species. Such information as is available additional to that we give about the locality and geological age of records taken from literature will be found in the works cited. We list below the localities from which we have seen specimens; for the many we have discussed in our previous papers we give references, and for the remainder we give such information as is available to us.

U.S.S.R.

'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, material of upper Eocene age (see Ross & Sims 1985: 280).

Anan'ino, Arkhangel'skoye-Kuroyedovo and Smol'kovo in Ulyanovsk oblast, material of Palaeocene age (see Ross & Sims, 1985: 280).

Simbirsk, now Ulyanovsk, Ulyanovsk oblast, used as an indication of the general district, material of Palaeocene age (see Ross & Sims, 1985: 280).

'Syzran'. Specimens so labelled very probably come from Palaeocene outcrops in Ulyanovsk oblast (see Ross & Sims, 1985: 280).

'Carlovo', presumed to be Karlovka, Kuibyshev oblast, material of Palaeocene or lower Eocene age (see Ross & Sims, 1985: 280).

'Isenski an der Wolga'. Part of a sample of material so labelled from the Hustedt collection was sent to the British Museum (Natural History) by Dr Simonsen. The only published mention of this locality is by Meister (1937: 259), who gives no details. We can find no place of this name in any gazetter of the U.S.S.R., and the nearest to it that might be 'an der Wolga' is Isheyevka, 54° 25′ N, 48° 16′ E, a small town a little north of Ulyanovsk, and we presume that 'Isenski' is a mis-transcription of this. Isheyevka is in an area where diatom-bearing rocks of Palaeocene and lower Eocene age outcrop.

Kutznetsk, Penza oblast, material of upper Eocene age (see Ross & Sims, 1985: 280).

Hungary

'Castel'. Specimens so labelled come from the outcrop of marine diatomite at Szurdokpüspöki, that is of upper Miocene age (see Chenevière, 1933, 1934: Holmes & Brigger, 1979).

Austria

We have seen specimens of *Trinacria cornuta* (Grev.) P. A. Sims & R. Ross from material

received from the late Mr A. L. Brigger labelled 'Austria, Oliogcene' for which no more information is available.

Denmark
Jutland, Glyngøre, Mors, Nykjøbing, and Fur, are the localities given for specimens from the Moler formation of lower Eocene (Ypresian) age (see Ross & Sims, 1987: 270).

North Atlantic Ocean
Blake Plateau, material of lower Eocene age from Deep Sea Drilling Project site 390 (see Gombos, 1982).

Haiti
Jérémie, material of lower Miocene age (see Ross & Sims, 1985: 284, where the suggestion that this material may be older is made).

Barbados
Cambridge, material of middle Eocene age (see Ross & Sims, 1985: 283).

Joe's River, Barbados, material from the Eocene to Oligocene boundary (see Ross & Sims, 1985: 283).

Chalky Mount, Mount Hillaby, Newcastle and Springfield, and specimens labelled only 'Barbados' are from the Oceanic Formation ranging from middle Eocene to lower Miocene (see Ross & Sims, 1985: 283–284).

South Atlantic Ocean
Falkland Plateau. Vema cruise 17, core 107, material of middle Eocene age (see Ross & Sims, 1985: 284), Deep Sea Drilling Project site 512, material of middle Eocene age (see Gombos, 1983: 565) and Vema cruise 18, core 112, material of Oligocene age (Fenner, personal communication).

'Lamont E 8'. The sample so labelled, received from the late Mr Brigger, is almost certainly from middle to upper Eocene material from the Falkland Plateau (see Ross & Sims, 1987: 271).

Arctic Ocean
Alpha Ridge. USGS site FI-437 and CESAR core 6. The silicoflagellate biostratigraphy of these two cores shows that they are of overlapping ages and indicates an upper Maastrichtian age with the upper parts of the cores possibly extending into the lower Palaeocene (Bukry, 1981, 1985; Kitchell et al., 1986). The paleomagnetic evidence agrees with this dating (Aksu, 1985). Barron (1985), however, considers that the diatom content suggests a Campanian age. In our view, the balance of evidence favours a Maastrichtian age and we accept that in this paper.

U.S.A.
Moreno Gulch, Fresno County, California, material of Maastrichtian age (see Ross & Sims, 1985: 282).

San Redondo and Santa Monica, Los Angeles County, California, material of lower Miocene age. According to Hanna (1936), samples labelled 'Redondo Beach' come from the outcrop of diatom-bearing shales at Malaga Cove and those labelled 'Santa Monica' from a detached block from this outcrop cast up on the shore at Santa Monica. This material comes from the upper part of the Monterey formation, which is of upper Miocene date (Hanna, 1928).

Terminology

The terminology used in the descriptions of taxa is that suggested by Anon. (1975) and Ross et al. (1979), with a few additions. 'Sibling valve' is defined by Ross & Sims (1985: 285), and 'interstrial pores' by von Stosch & Simonsen (1984: 11). 'Secondary pseudoseptum', 'marginal chamber' and 'buttress' are introduced here. At each apex of *Trinacria cancellata* (Grev.) P. A. Sims & R. Ross and *T. caudata* (Witt) P. A. Sims & R. Ross there is not only a well

developed pseudoseptum at about the level of the valve margin but also above this two or three similar but smaller silica projections from the walls of the valve (Figs 84, 94); these latter we call 'secondary pseudosepta'.

In the majority of the species with which we deal, and in many other species of *Trinacria*, the upper row of areolae on the mantle and the row on the valve face immediately adjacent to the marginal ridge do not open directly into the interior of the frustule. Each areola on the mantle is opposite one on the valve face and each pair opens into a chamber separated by walls on either side from the chambers into which adjacent pairs of areolae open. Each of these chambers opens into the interior of the frustule through a round hole in a sheet of silica that connects the valve face just proximal to the outermost row of areolae on it to the mantle just below its uppermost row of areolae. These chambers we call 'marginal chambers' (Latin: cubiculum, pl. cubicula). They are well shown in Figs 7 and 70. At times, usually on the middle part only of each side of the valve, there are no areolae on the valve face opening into the marginal chambers but only those on the mantle.

We use the word 'buttress' (Latin: fultura) for the structure at the base of the external tube of the labiate processes in the species with which we deal. These are flanges of silica tapering upwards attached to the tube of the labiate process that are shown in Figs 5 and 38. In some species they are extended over the valve face and unite to form external costae (Figs 19, 26).

In the latin description of *Trinacria barronii* P. A. Sims & R. Ross we use the word 'porca', (pl. porcae), literally the ridge formed between furrows in ploughing, for the low ridges between the areolae on the summits of the elevations in some specimens of this species. This word is not used there as a morphological term but only as an appropriate descriptive word for the contour of the valve surface in that place.

Description of species

All the species described below are members of the genus *Trinacria* Heiberg, one characteristic of which is that the external part of the labiate process is a tube projecting from the valve surface, a character which it shares with many other genera of the Biddulphiaceae. Here we deal with those species in which this external tube has buttresses at its base, these sometimes united to form external costae. Within some species there is considerable variation in the extent to which these buttresses are developed and also in the number and position of the labiate processes. The density of the areolae and the size of the valve also vary considerably but continuously. In some species, in particular *T. cornuta* (Grev.) P. A. Sims & R. Ross and *T. cancellata* (Grev.) P. A. Sims & R. Ross, the population in any one fossil deposit shows only a part of the range of variation of the species as a whole, but the degree of overlap between populations is such as to make any taxonomic separation impossible. Some characters, on the other hand, are constant within species: the presence or absence of marginal chambers, the number and arrangement of linking spines on each elevation, the presence or absence of a vertical external costa at each apex, the presence or absence of secondary pseudosepta, and the presence or absence of spines on the marginal ridge.

In the listings of the distribution of each species, we use entries in the form 'Palaeocene–lower Eocene' only when the age of the material is of uncertain position within those limits. When there is a continuous record from one locality that spans more than one period we use, e.g. 'lower to upper Eocene'.

The following is a key to those species of *Trinacria* with buttressed labiate processes:

1a. Valves quadripolar or 5-polar:
  2a. Vertical external costa at each apex:
    3a. 1–4 narrow radial folds on valve face ..... 3. ***T. cristata*** (p. 283)
    3b. No radial folds on valve face ..... 1. ***T. cornuta*** (p. 279)
  2b. No vertical external costa at each apex:
    4a. Apices narrowly rounded, not produced ..... 2. ***T. ecostata*** (p. 282)
    4b. Apices broadly rounded, produced ..... 7. ***T. barronii*** forma ***tetragona*** (p. 292)

1b. Valves tripolar:
5a. 3–9 short internal costae along each side of the valve, those near the apices sometimes uniting with those opposite ..... 4. ***T. cancellata*** (p. 285)
5b. No short internal costae along the sides of the valve:
6a. A circular costa or a hyaline ring bearing spines and 1–9 labiate processes surrounding the centre of the valve ..... 10. ***T. coronata*** (p. 298)
6b. No circular costa or hyaline ring:
7a. Buttresses of labiate processes united to form a single radiate pattern:
8a. 5–7 labiate processes; marginal ridge without spines ..... 5. ***T. interlineata*** (p. 288)
8b. 8–9 labiate processes; marginal ridge with spines ..... 6. ***T. fimbriata*** (p. 290)
7b. Buttresses of labiate processes not united to form a radiate pattern:
9a. 1 labiate process; secondary pseudosepta present ..... 9. ***T. caudata*** (p. 297)
9b. 2–15 labiate processes; no secondary pseudosepta:
10a. 2 labiate processes; apices produced and broadly rounded ..... 7. ***T. barronii*** forma ***barronii*** (p. 291)
10b. 3–15 labiate processes; apices not produced, narrowly rounded ..... 8. ***T. senta*** (p. 295)

1. **Trinacria cornuta** (Grev.) P. A. Sims & R. Ross, **comb. nov.**
(Pl. 1; Pl. 12 Figs 78, 79)

Triceratium cornutum Grev. in *Trans. microsc. Soc. Lond.* II, **9**: 45, 69, pl. 8 fig. 8 (1861). – Williams in *Bull. Brit. Mus. nat. Hist.* (Bot.) **18**: 52, pl. 60 fig. 4 (1988).

Triceratium acutangulum Grev. in *Trans. microsc. Soc. Lond.* II, **12**: 93, pl. 13 fig. 12 (1864). – Williams in *Bull. Brit. Mus. nat. Hist.* (Bot.) **18**: 51, pl. 58 figs 5, 8 (1988).

Trinacria excavata forma *tetragona* A. Schmidt, *Atlas Diat.*: Taf. 152 figs 26–28 (1890). – Paramonova in *Trudy vses. neft. nauchno-issled. geol.-razv. Inst.* **239**: 242, tabl. XI fig. 4 (1964). – Jousé, *Atlas Mikroorg. donn. osadk. Okean.*: tabl. 65 figs 13, 14 (1977). – Fenner in *Init. Rep. Deep Sea Drilling Proj.* **39**: 535, pl. 27 figs 9–11 (1977). – Dzhinoridze* et al. in *Init. Rep. Deep Sea Drilling Proj.*: Suppl. **38–41**: 314, 323, 326, pl. 10 fig. 5 (1978). –Dzhinoridze et al. in *Issled. Fauny Morei* **23** (31): 59, ris. 141–143 (1979). – Gombos in *Bacillaria* **5**: 227, figs 20–21 (1982); in *Init. Rep. Deep Sea Drilling Proj.* **71**: 571, pl. 4 fig. 11 (1983): in *Init. Rep. Deep Sea Drilling Proj.* **73**: 501, pl. 5 figs 7–9 (1984). – Baldauf in *Init. Rep. Deep. Sea Drilling Proj.* **81**: pl. 11 fig. 4 (1984). – Fenner in Bolli et al., *Plankton Stratigraphy*: 741, figs 8.29, 8.30 (1985).

Solium exsculptum sensu A. Schmidt, *Atlas Diat.*: Taf. 152 figs 24, 25 (1890), non Heiberg.

Amphitetras acutangula (Grev.) De Toni, *Syll. Alg.* **2**: 904 (1894).

Trinacria sp. Mukhina in *Okeanologiya* **14**: 856, ris. 2 fig. 15 (1974).

Trinacria quadrata H. J. Schrader & Fenner in *Init. Rep. Deep Sea Drilling Proj.* **38**: 1003 (1976), nom. nud. (Art. 32.1).

Trinacria excavata forma *inflata* Gombos in *Init. Rep. Deep Drilling Proj.* **71**: 572, pl. 4 figs 5–10 (1983).

Valves quadripolar or quinquepolar, with concave sides and acute to acuminate apices, length of side 17·5–145 μm, valve face slightly domed, occasionally depressed in the centre, height at the centre of the valve 9–17 μ,. Elevations tapering upwards in their lower parts, triangular in cross section, height to their summits 16–45 μm. A hyaline marginal ridge 1–1·5 μm tall continuous between the summits of the elevations. A hyaline vertical ridge or costa at each apex of the valve extending from the valve margin almost or quite to the summit of the elevation. Mantle vertical. A small hyaline area in the centre of the valve, 5–8 μm in diameter. Areolae poroid, 0·5–2·0 μm in diameter, occluded by cribra; on the valve face somewhat variable in diameter, in more or less regular radial rows extending to the summits of the elevations, 3–8 in 10 μm; on the mantle along the sides of the valve the areolae larger than elsewhere and in two horizontal rows, occasionally only one; on the mantle close to the apices and on the distal sides of the elevations the areolae irregularly arranged and smaller and closer than elsewhere, the nearer the summits of the elevations the smaller and closer; on the summits of the elevations a few small areolae *c.* 0·25 μm

* The second letter of this author's name is the seventh letter of the Cyrillic alphabet, normally transliterated 'zh' to distinguish it from the eighth letter transliterated 'z'. We have used the same spelling when referring to this publication as we have when transliterating from Cyrillic, although he used 'Dzinoridze' here.

in diameter. The upper row of areolae on the mantle and the outer row on the valve face opening into marginal chambers. Scattered interstrial pores present, their external rims often projecting as hollow spines up to 1 μm tall. Linking spines on each elevation either two continuing the marginal ridges or one in the centre of the proximal side of the summit, 1·5–4 μm tall; often also 1–3 shorter spines 0·5–1 μm tall on the distal edges of the summit. 1–3, occasionally 4, labiate processes on the valve face, the inner opening of each a straight slit 1–2 μm long across a papilla, the external part a thin tube, vertical or slightly inclined or curved, up to 15 μm tall, with 1–4 buttresses at the base extending up to 4 μm but often only slightly developed. Margin of the valve thickened, with small pseudosepta projecting *c.* 3 μm at the apices. Cingulum of at least three closed bands, the valvocopula *c.* 11 μm deep, the next copula *c.* 9 μm deep and the pleura *c.* 3·5 μm deep with bluntly rounded abvalvar projections *c.* 2 μm deep at each corner of the frustule. All girdle bands with small areolae *c.* 0·2 μm in diameter arranged in vertical rows, the rows 23 in 10 μm, the areolae *c.* 15 in 10 μm.

forma *cornuta*
Valves 4-polar.

Palaeocene. Indian Ocean, 14° 46·7′ S, 88° 54·4′ E, 4780 m depth. Vityaz station 6744-40 (Mukhina, 1974; Jousé, 1977).

Cape Basin, South Atlantic Ocean, 29° 29·055′ S, 3° 30·74′ E, 4805 m depth. Deep Sea Drilling Project site 524 (Gombos, 1984).

Lower Eocene. Island of Mors, Denmark (BM coll. Adams J3016, J3017, lectotype of *Trinacria excavata* forma *tetragona*, J3018; A. Schmidt, 1890).

Lower and middle Eocene. Blake Plateau, North Atlantic Ocean, 30° 08·54′ N, 76° 06·74′ W, 2665 m depth. Deep Sea Drilling Project site 390 (BRM Zu2/78; Gombos, 1982).

Lower Eocene–upper Eocene. Rockall Plateau, North Atlantic Ocean, 56° 02·56′ N, 23° 13·8′ W, 2311 m depth. Deep Sea Drilling Project site 552A (Baldauf, 1984).

Lower Eocene to transition to Oligocene. Plain between rivers Ob and Pur, and Tazovsk Peninsula, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).

Middle Eocene. Continental slope off U.S.A., North Atlantic Ocean, 38° 42·27′ N, 72° 39·21′ W, 1855 m depth. Deep Sea Drilling Project site 108 (Fenner, 1985).

Bermuda Rise, North Atlantic Ocean, 30° 50·39′ N, 67° 38·86′ W, 5125 m depth. Deep Sea Drilling Project site 6 (BM SEM 61693–61698).

Cambridge, Barbados (BM 2075, holotype, 3103, holotype of *Triceratium acutangulum*, 3117, 3134, 3139, 3281, 3446, 37736).

São Paulo Plateau, South Atlantic Ocean, 28° 17·22′ S, 41° 05·28′ W, 3203 m depth. Deep Sea Drilling Project site 356 (Fenner, 1977).

Falkland Plateau, South Atlantic Ocean, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 50 cm (BM SEM 35957–35962, 51606–51607), 120 cm (BM SEM 36019–36028, 36063–36054).

Falkland Plateau, South Atlantic Ocean, 49° 52·194′ S, 40° 50·713′ W, 1844 m depth. Deep Sea Drilling Project site 512 (BRM Zu2/74, holotype of *Trinacria excavata* forma *inflata*; Gombos, 1983).

Middle to upper Eocene boundary. Norwegian Sea, North Atlantic Ocean, 67° 47·11′ N, 5° 23·26′ E, 1297 m depth. Deep Sea Drilling Project site 338 (Schrader & Fenner, 1976; Dzhinoridze et al., 1978; Dzhinoridze, Jousé & Strel'nikova, 1979).

Middle Eocene–lower Miocene. Barbados (BM 10457, 37632, 52786, 58979).

Chalky Mount, Barbados (BM coll. Adams E654).

Mount Hillaby, Barbados (BM coll. Adams GC2741).

Springfield, Barbados (BM 37631, 37633, 37736, coll. Adams Bess. 1524).

Upper Eocene. Norwegian Sea, North Atlantic Ocean, 67° 12·65′ N, 6° 17·05′ E, 1262 m depth, and 64° 12·65′ N, 6° 18·34′ E, 1217 m depth. Deep Sea Drilling Project sites 339 and 340 (Dzhinoridze et al., 1978; Dzhinoridze, Jousé & Strel'nikova, 1979).

Kuznetsk, Penza oblast, U.S.S.R. (BM coll. Adams TS693).

'Kamichev' (presumed to be Kamyshlov, Sverdlovsk oblast), U.S.S.R. (BM 65821, 65831, SEM CB15.376–377, 36263–36277, 36787–36794, 36802–36803, 51563–51574).

Eocene to Oligocene boundary. Joe's River, Barbados (BM SEM 44538–44542).

Oligocene. Austria (BM SEM 44639–44644, 50771–50772).

forma **pentagona** P. A. Sims & R. Ross, **forma nov.**
Valvae quinquepolares.

Typus: BM 81486 ex stratis eocaenicis de profundis maris Atlantici australis.

Valves 5-polar

Middle Eocene. Falkland Plateau, South Atlantic Ocean, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 50 cm (BM SEM 24437–24440), 120 cm (BM SEM 36015–36018).

Middle–upper Eocene. Falkland Plateau, South Atlantic Ocean, 47° 45·7′ S, 57° 38·5′ W, 3650 m depth. Conrad cruise 12, core 237 (BM 81486).

Almost all the authors who have recorded *Trinacria cornuta* have called it *T. excavata* forma *tetragona*. A. Schmidt (1890), when publishing that name, illustrated three specimens; two of these, the originals of fig. 26 and fig. 28, are mounted on the same slide in BM (coll. Adams J3017), and we designate the specimen mounted in valve view, the original of fig. 26, as the lectotype. The specimens illustrated by A. Schmidt as fig. 24 and fig. 25 on the same plate, of which he said 'nach Witt's Ansicht vielleicht zu Solium exsculptum zu rechnen', are also in BM, both on slide coll. Adams J3016. They are obviously smaller examples of the same species.

Trinacria cornuta cannot be regarded as a quadripolar form of *T. excavata* Heiberg, a species which has three unbuttressed labiate processes, each about halfway between the centre of the valve and an apex, and which does not have a vertical costa at each apex (see Ross, Sims & Hasle, 1977: 190, pl. 8 figs 53–56).

Trinacria excavata forma *inflata* Gombos (1983) is based on specimens of *T. cornuta* with the elevations smaller in cross section than is normal in the species. One of us (R.R.) has examined its type (BM Zu2/74) and concluded that it is not sufficiently distinct from other specimens of the species to merit taxonomic separation even at the level of forma.

The principal difference between *Trinacria cornuta* and *T. ecostata* P. A. Sims & R. Ross, and the only one that can be detected with the light microscope, is the presence of vertical costae at the apices of the valve. It is not always easy to decide from published photomicrographs, especially those trimmed to the edge of the specimen, whether these costae are present. Nevertheless, whilst some of the specimens in BM that have been identified as *T. excavata* forma *tetragona* are *T. ecostata*, we believe that all the published figures seen by us that are so identified are of *T. cornuta*. None are of specimens from the Palaeocene or lower Eocene deposits of the middle Volga basin, from which come all the specimens of *T. ecostata* that we have seen.

Grunow published the names *Triceratium (Odontella) cornutum* var. *pulchellum* forma 5-gona (in Van Heurck, 1883: pl. 108 fig. 12) and *T. cornutum* var. *pulchellum* forma 4-gona (idem: pl. 108 fig. 13), based on recent specimens from the Seychelles Islands. A few years later the name *Triceratium pulchellum* Grunow ex A. Schmidt (1886a: Taf. 98 figs 16, 17) was published, also based on specimens from the Seychelles Islands but without any reference to the figures in Van Heurck (1883). It is clear, however, from the illustrations that they are of the same species, and recent specimens matching them show that this is one closely related to *Amphitetras antediluviana* Ehrenberg and not even congeneric with *Trinacria cornuta*.

Trinacria cornuta, as we have delimited it, has a wide range of size, and the closeness of the areolae also varies considerably, the smaller specimens tending to have closer areolae than the larger. Only part of this range is to be found in the specimens from any one locality but the overlap between populations is too great for any taxonomic separation based on differences in these characters. There is also variation in the number of labiate processes, in their position and in the extent to which the buttresses at their base are developed. The populations from different localities tend to be more uniform and have less overlap in these characters, but there is enough to preclude taxonomic separation at any level, as Table 1 shows. This table sets out the characteristics of the labiate processes for all the specimens that we have examined and all those illustrated by other authors in such a way that their labiate processes are visible, except for those from localities where only one such specimen is available. The figures in the column headed 'Offset from centre' are the fraction of the radius of the valve by which the process, when there is only one, is distant from the centre; when there is more than one process, these are at different distances but none is almost central. Small buttresses are those extending no more than 0·5 μm, medium ones those extending 0·5–1·0 μm, and large ones those extending more than 1 μm.

Trinacria cornuta forma *cornuta* is known from the Palaeocene to at least the Oligocene. Its

Palaeocene records are from the Indian Ocean and the Cape basin of the South Atlantic Ocean. Throughout the Eocene and up to at least the beginning of the Oligocene it had a wide distribution in the Atlantic basin and it also occurred throughout this period in the west Siberian Plain. In the middle Volga basin, however, it is known only from the upper Eocene, and it also occurs in the Oligocene of Austria. Although the specimen illustrated by Baldauf (1984: pl. 11 fig. 4) from the Rockall Plateau comes from an upper Pliocene level in the core from Deep Sea Drilling Project site 552A, he says of this: 'Reworking of Eocene, early Miocene and middle Miocene species occurs sporadically throughout the hole.' We have accordingly attributed an Eocene age to this specimen.

Trinacria cornuta forma *pentagona* has a much more restricted distribution. It is known only from the middle Eocene of the Falkland Plateau in the South Atlantic Ocean.

Table 1 Labiate processes of *Trinacria cornuta*

Age and locality	*Number of specimens*	*Number of processes*	*Offset from centre*	*Size of buttresses*
Palaeocene	*2*	*4*		*small*
Cape Basin	*1*	*1*	*7/8*	*small*
Lower Eocene				
Denmark	*4*	*1*	*< 1/8*	*small*
Lower Eocene				
Blake Plateau	*2*	*1*	*< 1/8*	*small*
Middle Eocene				
São Paulo Plateau	*2*	*1*	*< 1/8, 1/4*	*medium*
Middle Eocene				
Falkland Plateau	*9*	*1*	*1/2–3/4*	*small*
Middle–upper Eocene	*2*	*1*	*3/4*	*?*
Norwegian Sea	*2*	*4*		*medium*
Middle Eocene	*1*	*1*	*< 1/8*	*small*
Continental slope, U.S.A.	*1*	*1*	*1/2*	*medium*
Middle Eocene–	*7*	*3*		*small*
lower Miocene,	*5*	*2*		*small*
Barbados	*2*	*1*	*< 1/8*	*small*
Upper Eocene	*9*	*1*	*< 1/8*	*large*
'Kamichev'	*2*	*1*	*< 1/8*	*small*

2. **Trinacria ecostata** P. A. Sims & R. Ross, **sp. nov.**
(Pl. 2; Pl. 12 Fig. 80)

Valva quadripolaris, marginibus concavis, apicibus angustis rotundatis, lateribus 27–84 μm longis; frons parum tholiformis; altitudo ad centrum valvae c. 15 μm. Elevationes sursum angustatae usque ad vertices; altitudo ad vertices elevationum 19–22 μm. Crista marginalis valida c. 1 μm alta, inter vertices elevationum continua. Limbus verticalis. Areolae poroides, diam. 1–2 μm, cribris occlusae; in fronte in seriebus radialibus 2·5–5 in 10 μm vertices elevationum attingentibus plus minusve regulariter dispositae; in limbo in 1–3 seriebus dispositae, sed prope apices et in lateribus distalibus elevationum irregulariter dispositae et minores et plus approximatae quam alibi; in verticibus elevationum areolae paucae parvae. Areolae ad marginem frontis et eae in serie superiore in limbo oppositae et, interne, inter se costae parvae. Pori interstriales in fronte irregulariter dispersi. In elevatione unaquaque aut spinae ligantes duae cristas marginales prorogantes aut spina ligans una ad centrum lateris proximalis verticis, hae spinae 3–5·5 μm altae, et in margine distali verticis 3–6 spinae ligantes minores 0·25–1·0 μm altae. In fronte 1–2 rimoportulae, apertura interna recta trans papillam posita, pars externa tubus angustus ad 7 μm altus, basi fulturis parvis duis. Margo valvae incrassata, ad apices pseudoseptis parvis intrinsecus 2–3 μm extensis.

Typus: BM coll. Adams C960, ex stratis palaeocaenicis ad 'Smol'kovo, Ulyanovsk oblast, U.S.S.R.'

Valves quadripolar, with concave sides and narrow, rounded apices, length of side 27–84 μm, valve face slightly domed, height at the centre of the valve *c.* 15 μm. Elevations tapering upward to the summits; height to their summits 19–22 μm. A well-developed hyaline marginal ridge *c.* 1·0 μm tall continuous between the summits of the elevations. Mantle vertical. Areolae poroid, 1–2 μm in diameter, occluded by cribra; on the valve face in more or less regular radial rows 2·5–5 in 10 μm extending to the summits of the elevations; on the mantle in 1–3 rows, but near the apices and on the distal sides of the elevations irregularly arranged and smaller and closer than elsewhere; on the summits of the elevations a few small areolae. The areolae along the margin of the valve face and those in the upper row of the mantle opposite, with a small internal costa between each pair. Scattered interstrial pores present on the valve face. On each elevation either two linking spines 3–5·5 μm tall continuing the marginal ridges or a single equally tall linking spine in the centre of the proximal side of the summit, together with 3–6 smaller linking spines 0·25–1·0 μm tall on the distal margin of the summit. 1–2 labiate processes on the valve face, the inner opening a straight slit across a papilla, the outer opening a thin tube up to 7 μm tall with two small buttresses at the base. Margin of the valve thickened, with small pseudosepta projecting 2–3 μm at the apices.

Palaeocene. Anan'ino, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams F104).
Arkhangel'skoye Kuroyedovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams L1).
Smol'kovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams C960, J3662).
Ulyanovsk (formerly Simbirsk), Ulyanovsk oblast, U.S.S.R. (BM SEM 52073–52080, 52085–52086).
'Syzran', U.S.S.R. (for this locality see p. 276) (BM coll. Adams TS436, TS442).
Palaeocene–lower Eocene. 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R. (BM SEM 36581–36586).

Trinacria ecostata has no vertical costa at the apices of the valve, and the specific epithet has been chosen because of this. The absence of vertical costae is one of the two characters that distinguish this species from *T. cornuta* (Grev.) P. A. Sims & R. Ross. *T. ecostata* does not have fully developed marginal chambers; the free edges of the small internal costae along the margin of the valve are not expanded laterally to form such chambers; *T. cornuta* has fully developed marginal chambers, but this difference cannot be detected with the light microscope. We have distinguished the two at the specific level because their distributions do not overlap. *T. ecostata* is confined to the Palaeocene, and perhaps lower Eocene, of the middle Volga basin in the U.S.S.R. whilst *T. cornuta*, which has a much wider distribution in both time and space, does not occur there in deposits of that age, although it is present there in the upper Eocene.

3. **Trinacria cristata** Gombos in *Bacillaria* **5**: 234, figs 22–24 (1982).
(Pl. 12 Figs 81–83)

Solium princeps M. Peragallo in Tempère & H. Peragallo, *Diat. Monde ent.*: 346 (1912), nom. inval. (Art. 38.1).

Valves quadripolar, with slightly to moderately concave sides and acute or acuminate apices, length of side 35–70 μm, valve face slightly domed, elevations tapering upward in their lower parts, triangular in cross section, height to their summits *c.* 30 μm. A hyaline marginal ridge *c.* 1 μm tall continuous between the summits of the elevations. A hyaline vertical ridge or costa at each apex extending from the margin of the valve to the summit of the elevation. Mantle vertical. A small hyaline area at the centre of the valve, diameter 5–8 μm. Areolae poroid, *c.* 1 μm in diameter; on the valve face in radial rows, 4–7 in 10 μm, extending to the summits of the elevations; on the mantle along the sides of the valve in two horizontal rows, close to the apices and on the distal sides of the elevations irregularly arranged and slightly closer than elsewhere; a few small areolae on the summits of the elevations. Marginal chambers into which the outer row of areolae on the valve face, and the upper row on the mantle, open probably present. Scattered interstrial pores present. Linking spines on each elevation either two continuing the marginal ridges or one on the proximal margin of the summit, 1–1·5 μm tall. One labiate process at the centre of the valve, its inner opening a straight slit, its external part a vertical tube *c.* 12 μm tall with 2–4 buttresses at its base. 1–5 narrow outward folds of the valve face running from the

central area towards the centre of a side but not quite reaching the marginal ridge; when 5 present, 4 running from the central area to the centre of a side, the fifth close to but slightly diverging from one of these 4. Margin of the valve thickened, with small pseudosepta projecting *c.* 3 μm at the apices.

Lower Eocene. Blake Plateau, North Atlantic Ocean, 30° 08·54′ N, 76° 06·74′ W, 2665 m depth. Deep Sea Drilling Project site 390 (BRM Zu2/78; Gombos, 1982).
Middle Eocene–lower Miocene. Barbados (BM coll. Adams TS465).
Mount Hillaby, Barbados (BM coll. Adams F1260, GC2741, GC3133, H245, L204, TS491, BRM Hd2/60; Tempère & Peragallo, 1912).

We have not been able to obtain unmounted specimens of *Trinacria cristata* for examination with the scanning electron microscope, and we have seen only one specimen mounted in girdle view. Because of this we cannot be certain that marginal chambers are present, although observation with the light microscope strongly suggests that they are. Also, the figures we give for the height of the elevations and of the labiate processes are based on a single specimen and accordingly give no indication of the range that occurs.

It is only the presence of radial folds of the surface of the valve that distinguishes *Trinacria cristata* from *T. cornuta* (Grev.) P. A. Sims & R. Ross. That these structures are folds, and not 'fine hyaline ridges, or thickenings' as in the original description, is shown by the fact that areolae are involved in them, as Figs 81 and 83 demonstrate. The extent to which these folds are developed varies. There are usually four running from the central area almost to the marginal ridge, but there may be no more than one that stops well short of the marginal ridge (Fig. 82). A single character so variable in the extent to which it is expressed may seem an inadequate basis for specific separation, but there is continuous gradation within *T. cornuta* from specimens distinguished from the type of *T. cristata* (Gombos, 1982: fig. 24) by nothing more than the presence of folds to ones such as those from the same material identified by Gombos (1982: figs 20, 21) as *T. excavata* forma *tetragona*; not to separate these taxonomically would obviously be absurd.

The name *Solium princeps* was published with a minimal diagnosis: 'Forme a 4 cornes du *Trinacria princeps* Witt', and no illustration. The diagnosis would have been just sufficient to have given the name valid publication had it been a recent species. As it was based on fossil specimens and was published after 1 January 1912 (cf. Voss et al., 1983: Art. 38.1) without an illustration or figure, it is not validly published. Identification of the species to which it applies is not possible from the diagnosis itself, but two microscope slides, BM coll. Adams GC2741 and H245, mounted and labelled *Solium princeps* by Tempère and from the original locality, Mount Hillaby, Barbados, show that it was applied to *T. cristata*. This species cannot, however, be regarded as a quadripolar form of *T. princeps*, a synonym of *T. coronata* Witt; it does not have the circular costa penetrated by labiate processes that is a characteristic of that species. (See pp. 298–299 below).

According to Gombos (1982), *T. cristata* occurs in the lower Eocene but not the middle Eocene in the core from site 390 of the Deep Sea Drilling Project taken from the Blake Nose of the Blake Plateau in the western North Atlantic Ocean. The only other place where it is known to occur is the outcrop of the Oceanic Beds at Mount Hillaby in Barbados, from which we have seen a number of specimens. Whether the one specimen localized no more precisely than Barbados comes from this outcrop or another cannot be known. The Oceanic Beds of Barbados were deposited over a long period, from the middle Eocene to the lower Miocene, but the level in them of the material from Mount Hillaby is not known. The possibility that the base of the Oceanic Beds is earlier than currently supposed and that the specimens from Mount Hillaby are contemporary with those from the Blake Plateau cannot be completely discounted. If this is not so, the presence of *T. cristata* in the lower Eocene but not in the middle Eocene at site 390 and its occurrence at Mount Hillaby and probably not elsewhere in the Oceanic Beds of Barbados is a peculiar distribution. There is one slight difference in the populations from the two localities: in those specimens from site 390 the areolae are 6–7 in 10 μm, in those from Mount Hillaby they are 4–5 in 10 μm.

4. **Trinacria cancellata** (Grev.) P. A. Sims & R. Ross, **comb. nov.**
(Pl. 3; Pl. 12 Fig. 84)

Triceratium cancellatum Grev. in *Trans. microsc. Soc. Lond.* II, **13**: 9, pl. 2 fig. 17 (1865). – Williams in *Bull. Brit. Mus. nat. Hist.* (Bot.) **18**: 52, pl. 59 fig. 7 (1988).
Triceratium heibergianum Grunow in *Hedwigia* **5**: 145 (1866).
Triceratium jensenianum Grunow in *Hedwigia* **5**: 145 (1866). – A. Schmidt, *Atlas Diat.*: Taf. 77 figs 15, 16 (1882). – Paramonova in *Trudy vses. nauchno-issled. geol.-razv.* Inst. **239**: 241 (1964).
Triceratium maculatum Kitton in *J. Quekett microsc. Club.* **2**: 169, pl. 14 fig. 14 (1871).
Triceratium heibergii Grunow in Van Heurck, Syn. Diat. Belg.: pl. 112 fig 9–11 (1883), nom. superfl. (Art. 63.1). – Hustedt in A. Schmidt, *Atlas Diat.*: Taf. 467 figs 20–22 (1959). – Paramonova in *Trudy vses. nauchno-issled. geol.-razv. Inst.* **239**: 241, tabl. IX fig. 3 (1964). – Gombos in *Init. Rep. Deep Sea Drilling Proj.* **73**: 500, pl. 1 figs 1–12 (1984).
Triceratium sentum ['sectum'] sensu Hajós in *Init. Rep. Deep Sea Drilling Proj.* **29**: 930, pl. 8 figs 3, 4 (1975), non Witt.

Valve tripolar with straight or slightly concave sides, the apices narrowly rounded to produced and subcapitate, the valve face shallowly domed to almost flat, gradually depressed towards the apices and rising gently to the summits of the elevations, length of side 54–100 μm, height at the centre of the valve 15–20 μm. Elevations sometimes scarcely taller than the centre of the valve, their summits from sub-triangular to parallel-sided and rounded at the apices of the valve, 10–14 μm by 5–10 μm, height to the summits 16–25 μm. A hyaline marginal ridge continuous between the summits of the elevations, the upper edge in the centre of each side about level with the centre of the valve. Mantle vertical. 3–9 internal costae on each side of the valve projecting inwards 5–8 μm from the mantle, those nearest the apices occasionally continuous from margin to margin. Areolae poroid, 1–3 μm in diameter, probably occluded by cribra; on the valve face in radial rows extending to the summits of the elevations, 2–5 in 10 μm; on the mantle in 2–4 horizontal rows; at the corners of the valve rather smaller and closer than elsewhere; a few small areolae on the summits of the elevations. Scattered interstrial pores present on the valve face. Summits of the elevations surrounded by a low hyaline ridge, sometimes absent on the proximal side, and with very short blunt spines between the areolae. 2–4 labiate processes near the centre of the valve, the internal opening of each a straight longitudinal slit across a narrow papilla, the external part a narrow vertical tube arising from an external costa, these costae united to form a triradiate or 4-radiate pattern, or a single line when only two labiate processes are present; occasionally two labiate processes in an unbranched costa and one in another, occasionally also two labiate processes in separate short costae. Margin of the valve thickened, its free edge often vertically undulate, the undulations 3–4 in 10 μm, a pseudoseptum projecting 8–15 μm at each apex and two or three secondary pseudosepta projecting less far.

Cretaceous – Campanian to Maastrichtian. Campbell Plateau, South Pacific Ocean, 50° 26·34′ S, 176° 18·99′ E, 2837 m depth. Deep Sea Drilling Project site 275 (Hajós & Stradner, 1975).
Palaeocene. Cape Basin, South Atlantic Ocean, 29° 29·055′ S, 3° 30·74′ E, 4805 m depth. Deep Sea Drilling Project site 524 (Gombos, 1984).
Lower Eocene. Jutland, Denmark (BM 45388, coll. Adams GC3310, SEM 55784–55802; Grunow, 1866).
Glyngøre, Jutland, Denmark (BM 30847).
Island of Mors, Denmark (BM 61139, coll. Adams J2962).
Njkjøbing, Island of Mors, Denmark (BM SEM 55905–55918; Kitton, 1871; Grunow in Van Heurck, 1883; Hustedt in A. Schmidt, 1959).
Island of Fur, Denmark (BM 7744, 9608, 34291, coll. Adams F116).
? Åhus, Skåne, Sweden (Cleve-Euler, 1948).
Lower to upper Eocene. Plain between the rivers Ob and Pur, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).
Tazovsk Peninsula, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).
Middle Eocene. Bermuda Rise, North Atlantic Ocean, 30° 50·39′ N, 67° 38·86′ W, 5125 m depth. Deep Sea Drilling Project site 6 (BM SEM 61689–61692, 61699–61700).
Cambridge, Barbados (BM 3111, holotype, 55116, coll. Adams E660).
Middle Eocene–lower Miocene. Barbados (BM coll. Adams B556, H330, SEM 54648–54649, 54847–54849, 55325–55332; A. Schmidt, 1882).

Mount Hillaby, Barbados (BM coll. Adams GC3291).
Newcastle, Barbados (BM 73651).
Springfield, Barbados (BM 52794, 73567).
Upper Eocene. Kuznetsk, Penza oblast, U.S.S.R. (BM 61120).
Eocene to Oligocene boundary. Joe's River, Barbados (BM coll. Adams TS822, TS922, TS934).

This species clearly does not belong to the genus *Triceratium* Ehrenberg sensu stricto. We have placed it in *Trinacria* in spite of the fact that it does not possess pointed linking spines arising from the outer edge of the summits of the elevations, a character considered diagnostic of the genus. The absence of a pseudocellus precludes the assigning of it to *Sheshukovia* Glezer and there is no other established genus to which it might belong. The shape of the valve and the pattern of the areolation are virtually identical with those of *Trinacria barronii* P. A. Sims & R. Ross, *T. interlineata* J. A. Long et al., *T. fimbriata* P. A. Sims & R. Ross, *T. caudata* (Witt) P. A. Sims & R. Ross and *T. senta* (Witt) P. A. Sims & R. Ross, all species that, like *T. cancellata*, have labiate processes with buttresses. It also shares with *T. caudata* another unusual character, the presence of secondary pseudosepta at the apices. Also, some specimens of *T. barronii* have very short blunt spines amongst the areolae on the summits of the elevations similar to those in *T. cancellata*. Whilst internal costae projecting as far as those in *T. cancellata* are not found in other species of *Trinacria*, the structure along the margin of the valve that results from their presence is close to that in those species with a row of marginal chambers.

As this species has no linking spines, it is scarcely surprising that Greville (1865) and all subsequent authors have placed it in *Triceratium* rather than *Trinacria*. Greville's illustration of the type shows neither the two labiate processes arising from a single unbranched costa nor the short internal costae along the margin of the valve, both of which are present on the type specimen. He did, however, notice the internal costae, for his remarks on the species conclude with: 'There is a sort of indication of the commencement of vein-like lines, here and there at the margin, especially near the angles, which is shown by some of the cellule-walls becoming thickened for a short distance inwards.'

There are only two features of *Trinacria cancellata* in which there is any appreciable variation. One is the shape of the apices; there may be no change in direction of the margin of the valve at the proximal edge of the elevations (Fig. 16), or there may be an abrupt change at this point with a subcapitate apex distal to this (Fig. 17). There is a continuous gradation in this character and there is little difference in the range of variation between populations from the various deposits where the species occurs.

There is also variation in the number of labiate processes and the pattern of costae through which these penetrate. The one specimen from the upper Cretaceous of the South Pacific Ocean illustrated by Hajós & Stradner (1975: pl. 8 figs 3, 5; these figures show the same specimen rotated 120°) has triradiate costae penetrated by three labiate processes. So also has the one specimen we have seen from the middle Eocene of the Bermuda Rise in the North Atlantic Ocean. This is by far the commonest pattern in specimens from the lower Eocene Danish Moler formation, but some specimens from there have two labiate processes in an unbranched costa and a third one in a separate short unbranched costa. Other even rarer arrangements in specimens from that formation are: four labiate processes in 4-radiate costae; three labiate processes in triradiate costae plus one in a short unbranched costa; two labiate processes and a solid spine arising from triradiate costae; two labiate processes each in a single short unbranched costa. Almost all the specimens from Barbados have two labiate processes in a single unbranched costa, as has the one specimen we have seen from the upper Eocene of Kuznetsk, Penza oblast, U.S.S.R. This arrangement has not been found in any specimen from the Danish Moler formation. In a few specimens from Barbados, however, each of two labiate processes is in a separate short unbranched costa, an arrangement also found in Danish specimens. The illustrations of specimens from the upper Palaeocene of the Cape Basin, South Atlantic Ocean provided by Gombos (1984: pl. 1 figs 1–12) show that almost the whole range of variation, including the arrangements commonest in both the Danish Moler formation and the Oceanic Beds of Barbados, occurs in the material he studied. It does not seem possible, therefore, to base any taxonomic distinction on these differences.

Grunow (1866) originally described specimens of this species from the Danish Moler formation as two separate species, *Triceratium heibergianum* with triradiate costae and *T. jensenianum* in which these were not present. The latter name was presumably based on specimens in which the labiate processes arise from separate unbranched costae. The descriptions of these species were not accompanied by figures and when Grunow later (in Van Heurck, 1883) provided illustrations these showed both sorts under a single specific name, *T. heibergii*. This is obviously an altered spelling of *T. heibergianum* but, as there is no explicit indication of this, *T. heibergii* must be regarded as a new name. As Grunow quotes as a synonym the earlier validly published *T. maculatum* Kitton, *T. heibergii* is an illegitimate superfluous name. Nevertheless, subsequent authors have all used this illegitimate name rather than *T. heibergianum*. Witt (1886) misapplied the name *Triceratium heibergii* to specimens of *Trinacria senta* (Witt) P. A. Sims & R. Ross, but later realized his error and published the name *Triceratium sentum* Witt (in A. Schmidt, 1890) for the species which he had earlier erroneously called *T. heibergii*. However, as the published figures show, Witt's misidentification has been followed by a number of Russian authors. Specimens of *Trinacria senta* misidentified as *Triceratium heibergii* are illustrated by Proshkina-Lavrenko et al. (1949: tabl. 94 fig. 7) and Glezer et al. (1974: tabl. 14 fig. 7, tabl. 17 fig. 1), and *Triceratium heibergii* var. *rostratum* Jousé (1951*a*) is also based on *Trinacria senta*. On the other hand, Paramonova's figure (1964: tabl. IX fig. 3) of *Triceratium heibergii* is of a specimen of *Trinacria cancellata* with triradiate costae. In the same paper she also records *Triceratium jensenianum* Grunow, and one can thus assume that her records of this are based on specimens of *Trinacria cancellata* with unbranched costae.

Hajós & Stradner (1975: 930, pl. 8 figs 3, 4) made the opposite error. They identified as *Triceratium sentum* the specimen of *Trinacria cancellata* with triradiate costae from the upper Cretaceous of the South Pacific Ocean that has already been mentioned (p. 286), mis-spelling the epithet '*sectum*'.

Trinacria interlineata J. A. Long et al. also occurs in this upper Cretaceous material from the South Pacific Ocean. Hajós & Stradner (1975: 932) misidentified this as *T. tristictia* Hanna, but Jousé (1977: tabl. 83 fig. 1) applied the name *Triceratium heibergii* to a specimen of *Trinacria interlineata* from this material.

Grove & Sturt (1886: 329, pl. 19 fig. 19) applied the name *Triceratium cancellatum* to a species that they found in the upper Eocene deposit from Oamaru, New Zealand but, after examination of Greville's type, they realized that they had misapplied it. As a consequence they treated their species as new, calling it *T. pseudonervatum* Grove & Sturt (1887*b*: 136).

De Toni (1894: 884) confused *Triceratium heibergii* Grunow with the very different *Odontella heibergii* Grunow (1884: 58, Taf. V fig. 60), a large bipolar species also found in the Danish Moler formation. When publishing the latter, Grunow suggested that it and some other species might belong to a separate genus, for which he suggested the provisional name *Denticella*. De Toni adopted the name *Denticella*, giving it valid publication, and attributed the name *Denticella heibergii* to Grunow, who did not publish the combination even as a provisional name. De Toni added as a synonym '*Biddulphia heibergii* V. H. Syn. t. 112 f. 9–11'. These are the figures of *Trinacria cancellata* the legend to which reads 'TR.[iceratium] (*Biddulphia*) HEIBERGII Grunow'. This synonymy of De Toni's has never been questioned; it is still accepted by VanLandingham (1978: 4047), although comparison of the figures of *Triceratium heibergii* (= *Trinacria cancellata*) in Van Heurck (1883: pl. 112 figs 9–11) with those of *Odontella heibergii* provided by Grunow (1884: Taf. V fig. 60a–c) shows that the two are completely different species that cannot be regarded as even congeneric.

There are three published illustrations of specimens from Barbados that almost certainly represent *Trinacria cancellata*, but their quality is such that there cannot be complete confidence in this, and they have not been included in the synonymy of the species. They are: Walker & Chase, 1887: pl. 3 fig. 15, identified as *Triceratium jensenianum*; Walker & Chase, 1887: pl. 3 fig. 16, identified as *T. cancellatum* var. *minus* ('*minor*'); Laporte & Lefébure, 1929: pl. 1 fig. 3, identified as *T. jensenianum*.

Another doubtful record is that of *Triceratium heibergii* var. *subconvexum ('subconvexa')* Cleve-Euler (1948: 176, Taf. XI fig. 47a–c) from the lower Eocene of southern Sweden. The

outline of the valve, which is the character on which she based this variety, is within the range of continuous variation found in *Trinacria cancellata*. It is impossible to tell from the figures whether the 'charakteristische mehreckige Zeichnung' at the centre of the valve consists of triradiate costae penetrated by two or three labiate processes or of a single buttressed labiate process such as is found in *Trinacria caudata* (Witt) P. A. Sims & R. Ross. There is a slight indication in the figures of short marginal costae but this is far from definite. In view of the geographical position from which these specimens come and the fact that they are of the same geological age as the Danish Moler formation in which *T. cancellata*, but not *T. caudata*, occurs, it is much more likely that they are the former, but this cannot be considered certain without examination of the type.

Trinacria cancellata was a long-lived species. The first record is from the upper Cretaceous, in deposits from the South Pacific Ocean dating from about the boundary between the Campanian and the Maastrichtian. It occurs in the Palaeocene of the Cape Basin in the South Atlantic Ocean, the lower Eocene of Denmark and perhaps southern Sweden, the lower to upper Eocene of the west Siberian Plain and the upper Eocene of the middle Volga basin in the U.S.S.R. It also occurs in the middle Eocene of the Bermuda Rise in the western North Atlantic Ocean and in the Oceanic Beds of Barbados that range in age from the middle Eocene to the lower Miocene. Amongst the specimens of *Trinacria cancellata* from these beds there are some from Cambridge, which date from the middle Eocene, and some from Joe's River, which date from about the upper Eocene to Oligocene boundary. Others, which come from Mount Hillaby, Newcastle, and Springfield, cannot be assigned to any particular age within the span covered by the Oceanic Beds, and this is, of course, also true of those with no more precise locality than 'Barbados'.

We have seen a single specimen that purports to come from the upper Miocene of California, but we are uncertain whether this record can be accepted. It is on a 'type' slide of specimens from San Redondo (BM coll. Adams TS478). There seems to be no other record of the species from the much studied Miocene of California, which strongly suggests that the specimen is a contaminant. This view is reinforced by the fact that it has triradiate costae penetrated by three labiate processes, an arrangement found in none of the specimens seen by us that are or might be of upper Eocene or later date. However, Grunow (1868: 103) recorded *Triceratium cancellatum* from 'Polycistinen-Gestein von Nankoori', a lower Miocene deposit from the Nicobar Islands. We have seen no specimen from there and Grunow provided no figure. It seems unlikely that he was applying the name correctly for, if he had done so, he would have realized that the diatom he was applying it to belonged to the species he had named *T. jensenianum* only two years earlier and would have quoted that name as a synonym. Our conclusion must thus be that *Trinacria cancellata* existed from about the end of the Campanian until at least the early part of the Oligocene, and that it is possible, although doubtful, that it persisted later than this, until the Miocene.

5. **Trinacria interlineata** J. A. Long et al. in *J. Paleont.* **20**: 116, pl. 18 fig. 11 (1946).
(Pl. 4; Pl. 12 Figs 85–86)

Trinacria tristictia Hanna in *Occ. Pap. Calif. Acad. Sci.* **13**: 38 (1927), pro parte non typica; Hajós & Stradner in *Init. Rep. Deep Sea Drilling Proj.* **29**: 932, pl. 9 figs 5, 6 (1975); Harwood in *Mem. geol. Soc. Amer.* **169**: pl. 10 fig. 21 (1988).

Triceratium caudatum sensu Jousé, *Atlas Mikroorg. donn. osadk. Okean*: tabl. 81 fig. 5 (1977), non Witt.

Triceratium heibergii sensu Jousé, *Atlas Mikroorg. donn. osadk. Okean*: tabl. 83 fig. 1 (1977), non Grunow.

Valves tripolar with straight or slightly concave sides and triangular subacute apices, the valve face shallowly domed and abruptly depressed along the sides of the valve but more gradually opposite the apices, the dome extending more than half-way to the apices and separated from the elevations by a deep depression, length of side 40–80 μm, height at the centre of the valve *c.* 8 μm. Elevations tapering upward, their summits subcircular and *c.* 2 μm in diameter, height to the summits 15–20 μm. A hyaline marginal ridge continuous between the summits of the elevations, *c.* 2·5 μm tall along the sides of the valve where its upper edge is level. Mantle 5–8

μm tall, slightly idented at the base around the apices and rather more strongly along the sides of the valve, the mantle and the hyaline marginal ridge deeply indented opposite the depressions of the valve face proximal to the elevations, the hyaline marginal ridge at this point deeper than elsewhere. Areolae poroid, *c.* 0·5 μm in diameter, occluded by rotae with 2–5 spokes, the spokes usually linked by thin arcs of silica; on the valve face in radial rows 7–11 in 10 μm, extending to the summits of the elevations; on the mantle in one or two rows along the sides of the valve, larger than elsewhere and 5–7 in 10 μm, their vela with larger centres and more spokes than those on the valve face; at the apices on the mantle and the outer sides of the elevations in more or less horizontal rows, 7–10 in 10 μm; a few small areolae on the summits of the elevations. Scattered interstrial pores present. A ring of 6–10 linking spines *c.* 0·2 μm tall around the summit of each elevation. Three external costae radiating from the centre of the valve to the centre of each side, occasionally one of these costae replaced by two at a narrow angle to one another, or one of them missing, and three, usually weaker, costae directed towards the apices. 5–7 labiate processes present, one in each costa at ⅓–½ of the distance from the centre of the valve to an apex or the centre of a side, the internal opening of each a straight slit 0·6–1 μm long across a papilla, the external part a narrow vertical tube 7–10 μm tall. Margin of the valve somewhat thickened and projecting inwards at the apices to form small pseudosepta *c.* 2 μm deep.

Upper Cretaceous – Campanian to Maastrichtian. Campbell Plateau, South Pacific Ocean, 50° 26·34′ S, 176° 18·99′ E, 2837 m depth. Deep Sea Drilling Project site 275 (Hajós & Stradner, 1975; Jousé, 1977). – Maastrichtian. Moreno Gulch, Fresno County, California, U.S.A. (BM 35157, 35158, 35159, 63812, 81432, coll. Adams TS902, TS903, TS933, TS950, SEM 55333–55347, 55409–55414; Long, Fuge & Smith, 1946).

Upper Cretaceous – Maastrichtian to Palaeocene. Seymour Island, Antarctica, 64° 15′ S, 56° 45′ W (Harwood, 1988).

A remarkable characteristic of *Trinacria interlineata* is the way in which the mantle and marginal ridge are deeply indented opposite the depressions of the valve face proximal to the elevations. This feature seems to be unique to this species. External costae from which labiate processes arise are found in some other species of *Trinacria*, but the arrangement in *T. interlineata* is not found elsewhere, although that in *T. fimbriata* P. A. Sims & R. Ross is not very dissimilar. The pattern of these costae in *T. interlineata* is very uniform, the only variations being the occasional doubling of one costa directed towards the centre of a side of the valve or the absence of one of these, and the differences in the extent to which the costae directed towards the apices are developed; whilst these usually run most of the way from the centre to the outer edge of the domed part of the valve, they sometimes extend for only a short distance on either side of the labiate process. It should perhaps be noted that marginal chambers are not found in this species. The species that most closely resembles *T. interlineata* is *T. fimbriata* P. A. Sims & R. Ross, described below (p. 290). The differences between the two are discussed under that species.

It would seem that Hanna (1927) did not distinguish this species from *Trinacria tristictia* Hanna, for he remarks in his discussion of that species: 'often there are black radiating lines on the disk; presumably these are caused by some factor in the preservation because they are so often absent.' As Hanna's illustration of the holotype of *T. tristictia* (Hanna, 1927: pl. 5 fig. 11) shows, it does not have any radiating costae. Whilst some specimens in BM identified as *T. tristictia* are *T. interlineata*, others match Hanna's illustration well and are presumably that species. These specimens do not belong to *Trinacria*; the elevations at their apices, which are scarcely taller than the rest of the valve, are flat-topped but without any linking spines. Comparison of the illustrations of the holotypes of *T. tristictia* and *Lithodesmium margaritaceum* J. A. Long et al. (1946: pl. 17 fig. 16) shows that the two names are synonyms, and *Lithodesmium* is probably the genus to which the species belongs, although further investigation is needed to establish this with certainty.

Hajós (in Hajós & Stradner, 1975), presumably as a consequence of Hanna's remarks, applied the name *Trinacria tristictia* to specimens of *T. interlineata* from the upper Cretaceous of the Campbell Plateau in the south-west Pacific. Jousé (1977), however, misapplied the names

Triceratium caudatum Witt (*Trinacria caudata* (Witt) P. A. Sims & R. Ross) and *Triceratium heibergii* Grunow (*Trinacria cancellata* (Grev.) P. A. Sims & R. Ross) to specimens of *T. interlineata* from this material. Harwood (1988) made the same error of identification as Hajós & Stradner and his record of *T. tristictia* from the Maastrichtian to Danian of Seymour Island, Antarctica, is based on the occurrence of *T. interlineata* in these deposits.

Schulz (1935: 400), in his account of the Senonian diatom flora from the shores of Zatoka Gdanska (the Gulf of Danzig) recorded *Trinacria princeps* Witt, commenting: 'Bezeichend für die Art sind die unregelmässig verlaufenden längeren oder kürzeren Radialrippen, die konkaven Seiten und die rundlich spitzen Enden.' These remarks, in which no mention is made of the circular costa characteristic of *T. coronata* Witt, of which *T. princeps* is a synonym, together with the date of the material, suggest that it was *T. interlineata*, or possibly *T. fimbriata*, that he found in this deposit.

Apart from the possibility that *Trinacria interlineata* occurs in the Senonian from the southern Shore of the Baltic, it is known from only three localities: the Campbell Plateau in the south-west Pacific Ocean from deposits dated from about the Campanian–Maastrichtian boundary; the Moreno shale from Fresno County, California, U.S.A. of Maastrichtian age; and Seymour Island, Antarctica, from a little below and above the Maastrichtian–Danian (Cretaceous–Palaeocene) boundary. Our knowledge of the Cretaceous diatom flora is, however, still so limited that we cannot say how much further its distribution extended in time and space.

6. **Trinacria fimbriata** P. A. Sims & R. Ross, **sp. nov.**
(Pl. 5; Pl. 12 Figs 87–88)

Valva tripolaris, lateribus parum concavis, 54–73 μm longis, apicibus subacutis; frons ad centrum tholo hexagonali ad latera valvae cristae marginales attingenti sed apicibus opposito abrupte depresso et minus quam dimidium radii attingenti; altitudo ad centrum valvae c. 13 μm. Elevationes sursum angustatae, verticibus sub-triangularibus c. 3 μm diam.; altitudo ad vertices elevationum c. 25 μm. Crista marginalis valida hyalina inter vertices elevationum continua, secus latera valvae 1·5–2 μm alta et spinas validas c. 3 in 10 μm ferens. Limbus ad centrum uniuscuiusque lateris valvae c. 12 μm altus, depressioni elevationi proximali oppositus c. 4 μm altus, basi parum indentatus. Areolae poroides, cribris occlusae, diam. 0·5–1 μm; in fronte in seriebus radialibus vertices elevationum attingentibus, 6–8 in 10 μm; in limbo majores quam alibi, diam. 1·5–2 μm et 4–5 in 10 μm, partibus depressis frontis oppositae in serie una, centro valvae oppositae in seriebus quatuor dispositae; ad angulos valvae in seriebus horizontalibus aliquantum irregularibus c. 7 in 10 μm dispositae; in verticibus elevationum paucae parvaeque. Pori interstriales in fronte irregulariter dispersi. In vertice uniuscuiusque elevationis spina ligans una 2–3 μm alta cristam marginalem prorogans. 8–9 costae externe ab centro valvae radiantes, aliquae validiores quam aliae, rimoportula in unaquaque, ad ½–¾ spatii inter centrum valvae et marginem tholi posita; apertura interna rimportulae uniuscuiusque recta, c. 1 μm longa, trans papillam posita, pars externa tubus angustus verticalis vel parum curvatus usque ad 7·5 μm altus.

Typus: BM 81427, ex stratis cretaceis ad 'Moreno Gulch, Fresno County, California, U.S.A.'

Valve tripolar with slightly concave sides and subacute apices, with a hexagonal dome, its margins abruptly depressed opposite the apices but not along the sides of the valve, the dome extending less than half-way to the apices, length of side 54–73 μm, height at the centre of the valve *c.* 13 μm. Elevations tapering upwards, their summits sub-triangular and *c.* 3 μm in diameter, height to the summits *c.* 25 μm. A well-developed hyaline marginal ridge continuous between the summits of the elevations, 1·5–2 μm tall along the sides of the valve, where it bears stout spines *c.* 3 in 10 μm. Mantle *c.* 12 μm tall at the centre of each side of the valve, curving down to be *c.* 4 μm tall about half-way to the apices, slightly indented at the base. Areolae poroid, occluded by cribra, 0·5–1 μm in diameter; on the valve face in radial rows extending to the summits of the elevations, 6–8 in 10 μm; on the mantle larger than elsewhere, 1·5–2 μm in diameter and 4–5 in 10 μm, in a single row opposite the depressed parts of the valve face, in 4 rows in the central part of each side; at the corners of the valve in rather irregular horizontal rows and *c.* 7 in 10 μm; on the summits of the elevations a few small areolae present. Scattered interstrial pores on the valve face. On the summit of each elevation a single linking spine 2–3 μm tall and continuing a marginal ridge. 8–9 external costae radiating from the centre of the valve,

some stronger than others, with a labiate process in each at ½–¾ of the distance from the centre of the valve to the outer edge of the domed part of the valve face, the internal opening a straight slit *c.* 1 μm long across a papilla, the external part a vertical or slightly curved narrow tube up to 7·5 μm tall.

Upper Cretaceous – Maastrichtian. Moreno Gulch, Fresno County, California, U.S.A. (BM 81427, SEM 55403–55408, 61658–61664).

The row of spines arising from the marginal ridge, giving it a fimbriate appearance, is a very unusual character in *Trinacria*, and its presence in this species has prompted our choice of epithet. The only other species in which a similar structure occurs is *T. coronata* Witt. We have seen only three specimens of *T. fimbriata* and have examined only one under the scanning electron microscope. This specimen is considerably eroded but traces of cribra remain in some areolae. There is no doubt a greater range of dimensions within the species than is exhibited by these three specimens. *T. fimbriata*, like *T. interlineata* J. A. Long et al., does not possess marginal chambers.

There are considerable similarities between *T. fimbriata* and *T. interlineata*, but there are also a number of differences. In *T. fimbriata* there are more radiating costae; the central dome is abruptly separated from the depressed areas of the valve face proximal to the elevations, its edges there being vertical or even slightly undercut, whilst along the sides of the valve it extends to the marginal ridge without any appreciable dip; the mantle, in consequence, is much taller in the central part of the valve than it is nearer to the apices. In *T. interlineata* the central dome slopes down towards both the apices and the sides of the valve, and the upper edge of the mantle between the elevations is horizontal. In *T. fimbriata* there is no strong indentation of the marginal ridge and the mantle a little proximal to the elevations; there are spines arising from the marginal ridge and there is only one rather stout linking spine on each elevation. *T. interlineata* has the indentation of the mantle and marginal ridge, it has no spines arising from the marginal ridge, and it has several very small linking spines on each elevation. These differences are more than sufficient for one to regard the two as distinct species in spite of their general resemblances and similar distribution.

As we mentioned above under *Trinacria interlineata* (p. 290), it is possible that Schulz's (1935) record of *T. princeps* Witt from the Senonian of the shores of Zatoka Gdanska (the Gulf of Danzig) was based on specimens of *T. fimbriata*. However, all that is known for certain of its distribution is that it occurs in the Maastrichtian Moreno Shale of California, U.S.A., where it is far from common.

7. **Trinacria barronii** P. A. Sims & R. Ross, **sp. nov.**
(Pl. 6; Pl. 7 Figs 44–48; Pl. 13 Figs 89–90)

Valva tripolaris quadripolarisve, illae quadripolares interdum diagoniis inaequalibus, apicibus productis rotundatis, lateribus parum concavis, rectis, vel parum convexis, 25–50 μm longis; frons tholiformis; altitudo ad centrum valvae 8–12 μm. Elevationes usque ad vertices angustatae; altitudo ad vertices elevationum 15–17 μm. Crista marginalis valida inter vertices elevationum continua, centro valvae opposita *c.* 1 μm alta sed depressionibus frontis prope elevationes opposita 2–3 μm alta. Areolae poroides, cribris occlusae, diam. 0·5–1·5 μm, eae prope marginem frontis et eae in limbo plerumque majores quam eae alibi; in fronte aut irregulariter dispersae aut in seriebus radialibus indefinitis dispositae, vertices elevationum attingentes, 4–6 in 10 μm; in limbo in 1–4 seriebus horizontalibus secus latera valvae, ad angulos minores et plus approximatae quam alibi et in seriebus horizontalibus dispositae; in verticibus elevationum areolae paucae parvae interdum porcis humilibus radialibus separatae, interdum inter se papillis humilibus. Areolae ad marginem frontis et eae in serie superiore in limbo in cubicula marginalia aperientes. Pori interstriales, extrinsecus margine elevato, in fronte irregulariter dispersi. In elevatione unaquaque aut spinae ligantes duae cristas marginales prorogantes aut spina ligans una ad centrum lateris proximalis verticis, hae spinae 2–6 μm altae, et in margine distali verticis 3–7 papillae vel spinae ligantes minimae. Rimoportulae duae vel, in speciminibus quadripolaribus nonnullis, tres, in parte tholiformi frontis positae; apertura interna recta, 1–1·5 μm longa, trans papillam posita; pars externa tubus angustus ad 8 μm altus, basi fulturis 2–4 trans superficiem valvae 1–4 μm transeuntibus. Margo valvae incrassata, ad apices pseudoseptis parvis intrinsecus 1–2 μm extensis. Cingulum ex duis minimum taeniis constans, altera

c. 13 μm alta, altera plus distali *c.* 7 μm alta, ambabus areolis in seriebus verticalibus munitis, seriebus 12 in 10 μm, areolis 9 in 10 μm.

Typus: BM 81428, ex stratis cretaceis de profundo maris Arctici ad 'Alpha Ridge'.

Valves tripolar or quadripolar, the quadripolar ones sometimes with unequal diagonals, with produced rounded apices, the sides slightly concave to slightly convex, length of side 25–50 μm, valve face domed, height at the centre of the valve 8–12 μm. Elevations tapering upward, height to their summits 15–17 μm. A well-developed hyaline marginal ridge continuous between the summits of the elevations, *c.* 1 μm tall in the centre of each side of the valve and 2–3 μm tall opposite the depressions of the valve face proximal to the elevations. Areolae poroid, occluded by cribra, 0·5–1·5 μm in diameter, those near the margin of the valve face and those on the mantle usually larger than those elsewhere; on the valve face irregularly scattered or in rather indefinite radial rows, extending to the summits of the elevations, 4–6 in 10 μm; on the mantle in 1–4 horizontal rows along the sides of the valve, at the corners rather smaller and closer than elsewhere and in horizontal rows; on the summits of the elevations a few small areolae in radial rows sometimes separated by low ridges, sometimes with low papillae between them. The outer row of areolae on the valve face and the upper row on the mantle opening into marginal chambers. Scattered interstrial pores with a raised external rim on the valve face. On the summit of each elevation either two linking spines continuing the marginal ridges or a single linking spine in the centre of the proximal side, spines 2–6 μm tall; 3–7 papillae or very small linking spines on the distal edge of the summits of the elevations. Labiate processes 2, or in some quadripolar specimens 3, on the domed part of the valve face, the inner opening a straight slit 1–1·5 μm long across a papilla, the external part a vertical tube up to 8 μm tall with 2–4 buttresses extending 1–4 μm over the valve surface. Margin of the valve thickened with small pseudosepta projecting inwards for 1–2 μm at the apices. Girdle of at least two elements, one *c.* 13 μm deep proximal to one *c.* 7 μm deep, both with areolae in vertical rows, rows 12 in 10 μm, areolae 9 in 10 μm.

forma **barronii**

Valvae tripolares.

Valves tripolar.

Upper Cretaceous – Maastrichtian. Alpha Ridge, Arctic Ocean, 85° 50′ 0·41″ N, 109° 01′ 0·52″ W, 1365 m depth. CESAR core 6 (BM 81428, SEM 60395–60398, 60429, 60431).

Alpha Ridge, Arctic Ocean, 85° 59·87′ N, 129° 58·76′ W, 1584 m depth. USGS site FI-437 (BM SEM 51272–51283, 58449–58466).

forma **tetragona** P. A. Sims & R. Ross, **forma nov.**

Triceratium tessela sensu Barron in *Geol. Surv. Canada Paper* **84** – 22: 141, pl. 10.3 fig. 10 (1985), non Krotov.

Valvae quadripolares.

Typus: BM 81429, ex stratis cretaceis de profundo maris Arctici ad 'Alpha Ridge'.

Valves quadripolar.

Upper Cretaceous – Maastrichtian. Alpha Ridge, Arctic Ocean, 85° 50′ 0·41″ N, 109° 01′ 0·52″ W, 1365 m depth. CESAR core 6 (BM 81429, SEM 33160–33163, 58441–58448; Barron, 1985).

Alpha Ridge, Arctic Ocean, 85° 59·87′ N, 129° 58·76′ W, 1584 m depth, USGS site FI-437 (BM SEM 37038–37039, 37043–37045, 51260–51271, 58467–58478).

We have named this species after Dr J. A. Barron, who published the first account of the diatom flora of one of the two sites from which we have found it.

The most obvious distinguishing character of *Trinacria barronii* is the presence of two labiate processes, or on some quadripolar specimens three, with well-developed buttresses. These can be readily detected with the light microscope. Also, in *T. barronii* there are, on the elevations of one of each pair of sibling valves, two tall linking spines continuing the marginal ridges (Fig. 39); on the other valve of the pair there is a single tall linking spine on the proximal side of the summit

of each elevation (Fig. 40). The other linking spines around the distal edge of the summit of each elevation are very small and often scarcely developed at all. This character distinguishes *T. barronii* from a very similar species occurring in the same material that has no buttresses on its labiate processes and has a ring of linking spines of equal size around the summits of its elevations, two or three of them on the proximal side. This latter species is probably *T. indefinita* Jousé, although we are not certain of this identification.

There are two further features of *Trinacria barronii* to which special attention should be drawn. In most specimens the areolae on the mantle and the distal face of the elevations continue uninterrupted around the apex of the valve with some areolae at the apex itself (Fig. 40). In a few, however, there is a slight interruption of the rows of areolae resulting in a vertical interstria there (Fig. 43). The other noteworthy point is that often on the summits of the elevations there are low rounded ridges running in a radial direction between the areolae (Fig. 39). More rarely these ridges have rounded papillae on them.

Barron (1985) applied the name *Triceratium tessela* (A. I. Krotov) Strel'nikova to *Trinacria barronii* forma *tetragona*. His figure (pl. 10.3 fig. 10) makes this plain; it shows a specimen with the unequal diagonals characteristic of this forma. *Trinacria tessela* A. I. Krotov (1959: 108, fig. 5) is, however, a different species with a rather different outline and with much smaller areolae. Strel'nikova (1974: 84, tabl. XXIX figs 8–11) described and figured specimens of it from material of similar age to that in which Krotov found it and from the same region, the northern Ural mountains of the U.S.S.R. There is no indication on her figures of the characteristic buttressed labiate processes of *T. barronii*.

Barron also records and figures *Trinacria acutangula* Barron (1985: 141, pl. 10.3 figs 6, 8, 9) from the material in which we have found *T. barronii*. The specimen illustrated as fig. 6 seems to have no marginal ridge, but those shown in figs 8 and 9 might be *T. barronii*, although no buttressed labiate process is certainly visible on either figure. They are more probably the very similar tripolar *Trinacria* species with one or two labiate processes without buttresses and with a ring of linking spines of equal size surrounding the summits of the elevations mentioned above (this page). In any case the name *Trinacria acutangula* Barron is an avowed substitute for the illegitimate later homonym *Triceratium acutangulum* Strel'nikova (1974: 83, tabl. XXXII figs 1–10), non *T. acutangulum* Grev. (1864), and has the same type. This is a species with much more acute apices than *Trinacria barronii*. Examination with the scanning electron microscope of specimens from the material studied by Strel'nikova that match the type of *Triceratium acutangulum* shows that it has one or two labiate processes without buttresses and also that the structure of the cribra (Fig. 50) is different from that in *Trinacria barronii*.

It is perhaps appropriate to comment at this point that, whilst all the other specimens figured by Strel'nikova are of specimens conspecific with the holotype (tabl. XXXII fig. 2), tabl. XXXII fig. 7 is of an example of *Trinacria excavata* Heiberg. The three labiate processes each about half-way from the centre to an apex, and also the narrower but more rounded apices make this plain.

Another species of *Trinacria* that has been described from specimens of Cretaceous age is *T. indefinita* Jousé (1951*b*: 50, tabl. 2 fig. 5). This also was described from the upper Cretaceous of the northern Ural mountains. According to the original description, this species has 10–11 areolae in 10 μm and its sides are only 18–24 μm long. However, the figures, which are drawings not photomicrographs, show 5–8 areolae in 10 μm, and one of them, fig. 5a, has a side 38 μm long. On this figure there is an indication of two labiate processes, but the areolae are arranged in very regular radial rows. We have not been able to examine the type specimen and without seeing this we cannot be certain of the correct application of the name, nor even whether it is the description or the magnification given for the figures that is inaccurate.

Strel'nikova (1974: 82, tabl. XXX figs 1–29, tabl. XXXI figs 1–6) transferred *Trinacria indefinita* to *Triceratium* as *T. indefinitum* (Jousé) Strel'nikova; she considered that *Trinacria* was not generically distinct from *Triceratium*. She gave a description and provided many figures identified as this species, all based on specimens of a similar age to Jousé's and from the same area. Strel'nikova's figures show at least two different species. Tabl. XXX figs 18–25, 27–29 and tabl. XXXI fig. 5 are of specimens with small areolae not very regularly arranged, well

developed pseudosepta, and elevations that are very little raised and apparently have no linking spines. They are almost certainly of a species of *Sheshukovia* Glezer. Tabl. XXX fig. 26 shows a valve that is much more highly domed than in any of the other specimens identified as *Triceratium indefinitum*. It also seems to belong to *Sheshukovia* rather than *Trinacria*, but it almost certainly represents a different species from that shown in tabl. XXX figs 18–25. Tabl. XXX figs 1–17 and tabl. XXXI figs 1–4, 6 are of a species with larger areolae usually arranged in regular radial rows, with very small pseudosepta, if any, and with taller elevations bearing linking spines. A single labiate process, apparently without buttresses, is shown on figs 12, 13, 16, 17. We have examined with the scanning electron microscope a specimen from the material studied by Strel'nikova that agrees with her tabl. XXX figs 1–17 and tabl. XXXI figs 1–4, 6. This specimen (Fig. 49), with one unbuttressed labiate process, areolae in regular rows and 6 linking spines of equal height on each elevation is clearly not *T. barronii*. Its close resemblance to Jousé's fig. 5a together with the locality from which it comes suggests very strongly that it is *T. indefinita*. As we suggested above (p. 293) two of Barron's figures of *T. acutangula* (Barron 1985: pl. 10.3 figs 8.9) probably show this species.

Barron (1985: 141, pl. 10.3 figs 11, 12) also records *Triceratium indefinitum* from the Maastrichtian of the Alpha Ridge, Arctic Ocean. His figures show specimens with highly domed valves that may well be the same species as that illustrated by Strel'nikova (1974) as her tabl. XXX fig. 26. They are certainly not *Trinacria barronii*.

Three other species of *Trinacria* have been described from Cretaceous specimens: *Trinacria tristictia* Hanna, *T. interlineata* J. A. Long et al., and *T. negeviensis* Moshkovitz et al. (1983: 188, fig. 8a–c). The first two, which are discussed above under *T. interlineata* (p. 289), are very different from *T. barronii*. *T. negeviensis* is based on eroded specimens and the illustrations of it, two of which are scanning electron micrographs, show no labiate processes. Although similar to *T. barronii* in outline, *T. negeviensis* differs in having 8–9 areolae in 10 μm arranged in more regular rows than those of *T. barronii*. It is, as Moshkovitz et al. suggest, probably closer to *T. indefinita* Jousé than to any other species.

There are other records of tripolar *Trinacria* species from the upper Cretaceous which might be based on specimens of *T. barronii*, although in all cases this seems unlikely. Hanna (1927: pl. 5 figs 7–9) figures *T. insipiens* Witt from the Maastrichtian Moreno Shale of California. Specimens from that deposit that match his description and figure have no buttresses on their labiate processes and are probably *T. indefinita*. Schulz (1935: 399, Abb. I fig. 11*) records *T. excavata* Heiberg from the Senonian of the shores of Zatoka Gdanska (the Gulf of Danzig), remarking of it that 'Die Seiten waren nicht so scharf Konkav wie bei der typischen Form.' This is equally true, however, of the specimen of *T. excavata* misidentified as *Triceratium acutangulum* by Strel'nikova (1974: tabl XXXII fig. 7; see p. 293 above) and there is thus no reason why Schulz's identification should not be accurate. His figure is of a specimen in girdle view which might be any one of *T. excavata*, *T. acutangula*, *T. indefinita*, or *T. barronii*, with the last being, on geographical grounds, the least likely.

Hajós & Stradner (1975: 932) record a number of species of *Trinacria* from the upper Campanian to lower Maastrichtian of the Campbell Plateau in the south-western Pacific Ocean. Their illustrations show that it is only those identified as *T. insipiens* Witt (pl. 10 figs 5, 6) or as *T. pileolus* Ehrenb. (pl. 9 figs 7, 8) that might be based on misidentified specimens of *T. barronii*. A single labiate process is visible on one of the figures of *T. insipiens* (pl. 10 fig. 5) but there is no indication of buttresses on it. The one specimen identified as *T. pileolus* (pl. 9 figs 7 and 8 both show the same specimen) has a central areola surrounded by a rosette-like ring of areolae, an arrangement we have not seen in *T. barronii*, and no labiate process can be seen on this specimen. It is thus very unlikely that *T. barronii* occurs in their material.

We accordingly conclude that the only certain records of *Trinacria barronii* are those from the Alpha Ridge in the Arctic Ocean, and that the specimens from there are of Maastrichtian age, possibly extending into the lower Palaeocene, as the species occurs throughout both cores (see p. 277).

* The legends of Abb. I and Abb. II in Schulz's paper are transposed.

8. **Trinacria senta** (Witt) P. A. Sims & R. Ross, **comb. nov.**
(Pl. 8; Pl. 13 Figs 91–92)

Triceratium sentum Witt in A. Schmidt, *Atlas Diat.*: Taf. 150 figs 2–6 (1890). – Harwood in *Mem. geol. Soc. Amer.* **169**: pl. 10 figs 1–3 (1988).

Triceratium heibergii sensu Witt in *Zap. imp. miner. Obshch.* II, **22**: 169, Taf. XI fig. 4 (1886), non Grunow. – Proshkina-Lavrenko et al., *Diat. Analiz* **2**: 164, tabl. 94 fig. 7 (1949). – Glezer et al., *Diat. Vodor. S S S R* **1**: tabl. 14 fig. 7, tabl. 17 fig. 1 (1974).

Triceratium venosum forma *majus* ['*major*'] A. Schmidt, *Atlas Diat.*: Taf. 150 fig. 1 (1890).

Trinacria venosa forma *major* (A. Schmidt) Van Heurck in *Res. Voy. S. Y. Belgica 1897–1899, Bot., Diat.*: 38, pl. 9 fig. 121 (1909).

Triceratium heibergii var. *rostratum* ['*rostrata*'] Jousé in *Bot. Mater. Otd. sporov. Rast. bot. Inst. Komarova, Akad. Nauk SSSR* **7**: 33, tabl. 3 fig. 1 (1951).

Triceratium sentum forma *majus* ['*major*'] Hustedt ex Simonsen, *Atlas & Catal. Diatom Types F. Hustedt* **1**: 466 (1987); *op cit.* **3**: pl. 701 figs 1–5 (1987). – Hustedt in A. Schmidt, *Atlas Diat.*: Taf. 467 figs 25, 26 (1959), nom. inval., sine design. typi (Art. 37.1).

Valves tripolar with slightly concave sides and acutely rounded apices, close to which the valve is sometimes slightly constricted, length of side 25–150 μm, surface domed, height at the centre of the valve 14–22 μm. Elevations tapering upward, height to their summits 16–43 μm. A well-defined hyaline marginal ridge 2–3 μm tall continuous between the summits of the elevations. Mantle vertical except for a slight indentation immediately adjacent to the valve margin. Areolae poroid, 1–2 μm in diameter, occluded by cribra; on the valve face in radial rows extending to the summits of the elevations, 2–6 in 10 μm; on the mantle in 2–3 rows along the sides of the valve, at the corners of the valve smaller and closer than elsewhere and in horizontal rows; on the summits of the elevations a few small areolae *c.* 0·3 μm in diameter. The outer row of areolae on the valve face and the upper row on the mantle opening into marginal chambers, these areolae and the other areolae on the mantle sometimes occluded by thin plates of silica. Scattered interstrial pores with raised external margins present on the valve face. A ring of 6–10 short triangular linking spines 1–2·5 μm tall surrounding the summits of the elevations. Labiate processes 3–15, the inner opening of each a straight slit *c.* 1 μm long across a papilliform projection, the external part a vertical or slightly curved tube up to 18 μm tall usually with 3–4 buttresses extending 5–15 μm over the valve surface as costae but not normally uniting with those from other labiate processes, occasionally with only two small opposite buttresses extending 1–1·5 μm. Margin of the valve thickened and extended inwards at the apices to form pseudosepta projecting *c.* 5 μm.

Upper Cretaceous – Maastrichtian to Palaeocene. Seymour Island, Antarctica, 64° 15′ S, 56° 45′ W (Harwood, 1988).

Palaeocene. Middle Volga Basin, U.S.S.R. (Glezer et al., 1974).

Anan'ino, Ulyanovsk oblast, U.S.S.R. (BM 61238, 63733, coll. Adams F104, G464).

Arkhangel'skoye Kuroyedovo, Ulyanovsk oblast, U.S.S.R. (BM Coll. Adams J1036, J1240; Witt, 1886; A. Schmidt, 1890).

Smol'kovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams C908; Hustedt in A. Schmidt, 1959).

Ulyanovsk (formerly Simbirsk), Ulyanovsk oblast, U.S.S.R. (BM 7702, 7751, 38030, 44213, 44214, 52962, 73836, 75947, 75948, 76079, coll. Adams Bess. 602, Bess. 1300, J663, TS10, SEM 52087–52092, 52099–52102, 52106, 52111; A. Schmidt, 1890).

'Syzran', U.S.S.R. (for this locality see p. 276). (BM 38031, 38107, coll. Adams Bess. 1668, TS439).

Eastern slope of the Ural mountains, U.S.S.R. (Glezer et al., 1974).

Sverdlovsk oblast, U.S.S.R. (Proshkina-Lavrenko et al., 1949).

Polunochnoye, Sverdlovsk oblast, U.S.S.R. (Jousé, 1951*a*).

Palaeocene–lower Eocene. 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R. (BM SEM 51587–51596, 56161–56164).

Eocene–Oligocene. Amundsen Sea, Antarctic Ocean, 70° 50′ S, 102° 13′ W, 1195 m depth. Expedition Antarctique Belge, sondage 58 (Van Heurck, 1909).

Middle Eocene. Falkland Plateau, south-western Atlantic Ocean, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 120 cm (BM SEM 53519–53525).

Oligocene. Falkland Plateau, south-western Atlantic Ocean, 51° 40′ S, 48° 29′ W, 2429 m depth. Vema cruise 18, core 112, 100 cm. (BM SEM 54179–54182, 55316–55324).

Lower Miocene? Jérémie, Haiti (BM coll. Adams TS96).

The pattern made by the buttresses of the labiate processes of *Trinacria senta* is so distinctive that the species is very readily recognized. Nevertheless, when Witt first recorded it in 1886 he misidentified it as *Triceratium heibergii* Grunow, an illegitimate name for *Trinacria cancellata* (Grev.) P. A. Sims & R. Ross. In spite of the fact that Witt realized his error and four years later published the name *Triceratium sentum* for the species in A. Schmidt's *Atlas der Diatomaceenkunde* along with further illustrations of it (Taf. 150 figs 2–6), Russian authors have continued to call it by the illegitimate name that Witt first, and incorrectly, used for it. In this they have followed Proshkina-Lavrenko et al. (1949), in which both *Triceratium maculatum* Kitton and *T. sentum* Witt are given as synonyms of *T. heibergii*. *T. maculatum*, like *T. heibergii*, is a synonym of *Trinacria cancellata*. Jousé (1951*a*) based her *Triceratium heibergii* var. *rostratum* on specimens of *Trinacria senta* in which the constriction of the valve just proximal to the apices is particularly marked. There is a continuous gradation in this feature and no taxonomic distinction can be based on it.

There is a very wide range of size in *Trinacria senta* and, in general, the larger the valve the more labiate processes are present. The specimens illustrated as *Triceratium sentum* when that name was first published (Schmidt, 1890: Taf. 150 figs 2–6) come from the smaller part of the size range. At the same time Schmidt illustrated a specimen of about the maximum size of the species (Taf. 150 fig. 1). He presumably had not seen any intermediates and so did not recognize its identity with *T. sentum*; instead he published for it the name *T. venosum* forma *majus*. It is, however, in no way related to *T. venosum* Brightwell, a species with pseudocelli but no linking spines on its elevations and with internal parallel costae, not external ones radiating from labiate processes. Van Heurck (1909) found a similar large specimen in material from a sounding taken from near Thurston Island, Antarctica. He realized it was a *Trinacria* but identified it with *Triceratium venosum* forma *majus*; he accordingly transferred Brightwell's species to *Trinacria* and made the appropriate combination for the forma. He recorded *Triceratium sentum* from the same sounding.

In *Trinacria senta*, as in *T. caudata* (Witt) P. A. Sims & R. Ross, *T. cancellata* (Grev.) P. A. Sims & R. Ross, and *T. cornuta* (Grev.) P. A. Sims & R. Ross, the degree to which the buttresses of the labiate processes are developed varies. It is only the specimens with poorly developed buttresses, such as that shown in Fig. 57, that present any difficulty in identification. Witt (1886) described *Triceratium nobile* Witt, *Triceratium grevillei* Witt, and *Trinacria grunowii* Witt from the Palaeocene deposit at Arkhangel'skoye Kuroyedovo, in which he also found *Trinacria senta*. Witt's illustrations of these three species, and examination of specimens from the type locality that match them, suggests that they are synonyms; they differ from each other only in the density of the areolae and there seems to be continuous variation in this. The only character that separates them from *T. senta* is the absence of buttresses on the labiate processes. This raises the question of whether this is an adequate basis for taxonomic separation, especially as some specimens of *T. senta* have poorly developed buttresses. For the present, however, we consider it best to treat as separate species those with and those without buttresses, at least until more is known about the distribution in time and space of the two forms.

Trinacria caudata (Witt) P. A. Sims & R. Ross, described below (p. 297) is a very similar species with only one buttressed labiate process, that is also found in the Palaeocene deposit at Arkhangel'skoye Kuroyedovo. Its existence, however, cannot be taken as indicating that there is a single species with the number of its labiate processes ranging from one to fifteen. *T. caudata* has secondary pseudosepta, *T. senta* does not.

The earliest record of *Trinacria senta* is from the late Maastrichtian and early Danian of Seymour Island, Antarctica (Harwood, 1988). Harwood also records *Triceratium heibergii* var. *rostratum* Jousé, a synonym of *Trinacria senta*, from the same deposit, but his illustration shows that he misapplied the name to a quite different species that we cannot at present identify. The record by Hajós & Stradner (1975) from the upper Campanian to lower Maastrichtian of the Campbell Plateau in the south-western Pacific Ocean is based on a misidentification (see p. 287 above under *T. cancellata* (Grev.) P. A. Sims & R. Ross). We have found *T. senta* in both

middle Eocene and Oligocene material recovered from the Falkland Plateau, and Van Heurck (1909) found it in material of Eocene or Oligocene date from close to Thurston Island, Antarctica. *T. senta* has also been found in the Palaeocene and possibly also the lower Eocene of the middle Volga basin and the eastern slopes of the Ural mountains, both in the U.S.S.R. We have also seen one specimen from Jérémie, Haiti, from a deposit that is probably lower Miocene in age. In this specimen the distal edges of the central dome opposite the apices are vertical, whilst those of all the other specimens we have seen slope more gradually. Whilst this by itself is not a difference sufficient to be the basis of any taxonomic separation, it does make it extremely unlikely that this specimen is a contaminant from some other locality. The known distribution of *T. senta* is thus from close to the top of the Cretaceous to the Oligocene in the western part of the Antarctic Ocean and the south-western part of the Atlantic Ocean, in the Palaeocene and possibly lower Eocene of the middle Volga basin and the Ural mountains of the U.S.S.R. and from the lower Miocene, or perhaps earlier, of the Caribbean, a distribution that can only be explained by the incompleteness of the fossil record.

It is possible that *Triceratium insuave* forma *trigona* Truan & Witt (1888: 24, Taf. VII fig. 9), from Jérémie, Haiti, is based on a specimen of this species but its identity is doubtful. Both the description and the illustration are inconclusive and the specimen from Jérémie that we have seen does not match either at all closely.

9. **Trinacria caudata** (Witt) P. A. Sims & R. Ross, **comb. nov.**
(Pl. 10; Pl. 13 Figs 93–94)

Triceratium caudatum Witt in *Zap. imp. miner. Obshch.* II, **22**: 168, Taf. XI fig. 4 (1886). – A. Schmidt, *Atlas Diat.*: Taf. 111 figs 18–23 (1886). – Proshkina-Lavrenko et al., *Diat. Analiz* **2**: 164, tabl. 94 fig. 4 (1949). – Glezer et al., *Diat. Vodor. S S S R* **1**: tabl. XV fig. 2 (1974).

Valve tripolar with slightly concave sides and narrowly rounded apices, length of side 40–110 μm, valve face domed, height at the centre of the valve 10–14 μm. Elevations tapering upwards, height to their summits 16–30 μm. A well-developed hyaline marginal ridge *c.* 1·5 μm tall continuous between the summits of the elevations. Mantle vertical. Areolae poroid, 1–2 μm in diameter, occluded by cribra; on the valve face irregularly arranged or in radial rows, extending to the summits of the elevations, 2·5–4 in 10 μm, a hyaline central area 4·5–7·5 μm in diameter usually present; on the mantle in 2–3 rows along the sides of the valve; at the corners of the valve smaller and closer than elsewhere and irregularly arranged or in horizontal rows; a few small areolae, 0·3–0·5 μm in diameter, on the summits of the elevations. The outer row of areolae on the valve face and the upper row on the mantle opening into marginal chambers. Scattered interstrial pores on the valve face. A ring of 8–12 short triangular linking spines 1–2 μm tall surrounding the summits of the elevations, those on the proximal side rather larger than the others, sometimes much larger and up to 6 μm tall. A single labiate process between the centre of the valve and the middle of one side, its distance from the centre variable, its inner opening a straight slit *c.* 1 μm long across a papilla, its external part a vertical or slightly inclined tube more than 6 μm tall, with 2–4 buttresses at its base extending for 1–8 μm across the the valve surface. Margin of the valve thickened and extended inwards as a pseudoseptum projecting 8–10 μm at the apices; two smaller secondary pseudosepta projecting less far at each apex.

Palaeocene. Middle Volga basin, U.S.S.R. (Glezer et al., 1974).
Ulyanovsk oblast, U.S.S.R. (Proshkina-Lavrenko et al., 1949).
Arkhangel'skoye-Kuroyedovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams J1241, W996; Witt, 1886; A. Schmidt, 1886*b*).
Ulyanovsk (formerly Simbirsk), Ulyanovsk oblast, U.S.S.R. (BM 63486, SEM 52081–52084, 52103–52105, 52107–52110, 57023–57030).
Palaeocene–Eocene. 'Isenski an der Wolga', (possibly Isheyevka, Ulyanovsk oblast), U.S.S.R. (BRM Hd2/84; BM SEM 48434–48443, 48445–48448, 48451–48453, 48456–48457).
Lower Miocene. Jérémie, Haiti (BM coll. Adams TS96).
Upper Miocene. San Redondo, Los Angeles County, California, U.S.A. (BM coll. Adams Bess. 878).
Santa Monica, Los Angeles County, California, U.S.A. (BM coll. Adams TS466).

Trinacria caudata is the only tripolar species of the genus that has a single buttressed labiate process, a character it shares with the quadripolar species *T. cornuta* (Grev.) P. A. Sims & R. Ross, *T. ecostata* P. A. Sims & R. Ross, and *T. cristata* Gombos. There can, however, be no question of regarding *T. caudata* and any one of these as tripolar and quadripolar forms of the same species. Both *T. cornuta* and *T. cristata* have a vertical external costa at each apex, whereas *T. caudata* does not, and *T. ecostata* has scarcely developed pseudosepta and no secondary pseudosepta at the apices, whilst *T. caudata* has well-developed pseudosepta and also secondary pseudosepta. All the three quadripolar species have two linking spines continuing the marginal ridges on one of each pair of sibling valves and a single spine in the centre of the proximal side of the summit of the elevations on the other member of the pair. The arrangement in *T. caudata* is different: on each elevation one marginal ridge is continued by a linking spine and the other finishes with an indentation where a linking spine from the sibling valve abuts against it; between these, on the proximal side of the elevation, is another linking spine and another indentation (Figs 67, 68).

The secondary pseudosepta that are found in this species are a very unusual character. The only other species that possess them are *Trinacria cancellata* (Grev.) P. A. Sims & R. Ross and *T. insipiens* Witt, if the latter is distinct from *T. caudata*. *T. insipiens* Witt (1886: 36, Taf. XI figs 5, 7, 11, Taf. XII fig. 2) differs from *T. caudata* only in the absence of buttresses on its labiate processes, and the extent to which these buttresses are developed in *T. caudata* is very variable. It may well be that the two should not be regarded as distinct, but we are for the present treating them as separate species.

As we have pointed out under *Trinacria cancellata* (p. 287), it is possible that *Triceratium heibergii* var. *subconvexum* Cleve-Euler (1948), from the lower Eocene of southern Sweden is based on specimens of *Trinacria caudata*, although it is much more likely to be a synonym of *T. cancellata*.

Trinacria caudata almost certainly has a wider distribution than that evidenced by the specimens that we have seen and the published records accompanied by illustrations. There is, for instance, little reason to doubt that Paramonova's (1964) record of *Triceratium caudatum* from the middle Eocene of the west Siberian Plain, U.S.S.R., is based on correctly identified specimens. However, the specimen from the upper Cretaceous of the Campbell Plateau in the South Pacific Ocean identified by Jousé as *T. caudatum* (1977: tabl. 81 fig. 5) is *Trinacria interlineata* J. A. Long et al. The certain distribution of this species, from the Palaeocene and possibly Eocene of the middle Volga basin in the U.S.S.R., the lower Miocene of the Caribbean and the upper Miocene of California, U.S.A., is peculiar, although it is to some extent paralleled by that of *T. cancellata* and *T. senta* (Witt) P. A. Sims & R. Ross.

10. **Trinacria coronata** Witt in *Zap. imp. miner. Obshch.* II, **22**: 171, Taf. X figs 5, 8 (1886). – A. Schmidt, *Atlas Diat.*: Taf. 110 figs 8–10 (1886). – Lefébure, *Atlas Déterm. Diat.*: pl. XX fig. 7 (1947). – Proshkina-Lavrenko et al., *Diat. Analiz* **2**: 194, tabl. 74 fig. 4a, b (1949).
(Pl. 11; Pl. 13 Figs 95–96)

T. princeps Witt in *Zap. imp. miner. Obshch.* II, **22**: 172, Taf. X fig. 9 (1886). – A. Schmidt, *Atlas Diat.*: Taf. 110 figs 15–17 (1886). – Proshkina-Lavrenko et al., *Diat. Analiz* **2**: 194, tabl. 73 fig. 10 (1949).

Hemiaulus coronatus (Witt) M. Peragallo, *Catal. Gén. Diat.*: 434 (1901), non *H. coronatus* Leuduger-Fortmorel (1898).

H. princeps (Witt) M. Peragallo, *Catal. Gén. Diat.*: 438 (1901).

Trinacria subcoronata Sheshukova-Poretskaya & Glezer in *Nov. Sist. Nizsh. Rast.* 1964: 88, tabl. IV figs 3–5 (1964). – Glezer et al., *Diat. Vodor. SSSR.* **1**: tabl. XXXVI fig. 4 (1974).

Triceratium coronatum (Witt) Strel'nikova, *Diat. pozdn. Mela (Zap. Sibir')*: 89 (1974), excl. descr. et fig.

Valve tripolar with straight or slightly concave sides and subacute apices, the valve face shallowly domed but with a slightly depressed circular area in the centre, length of side 37–160 μm, height at the centre of the valve *c.* 15 μm. Elevations tapering slightly upward, their summits sub-triangular, *c.* 4 μm in diameter, height to the summits 40–50 μm. Hyaline marginal

ridges continuous between the summits of the elevations, 0·5 μm or less tall on the elevations, 6–8 μm tall along the sides of the valve and bearing spines 6–8 μm apart and up to 15 μm tall. Mantle 8–10 μm tall, slightly concave. Areolae slightly locular with an external cribrum, those on the valve face 1·5–2·0 μm in diameter and with an internal foramen 1·2–1·8 μm in diameter, in radial rows on the valve face extending to the summits of the elevations, 3–6 in 10 μm; on the mantle along the sides of the valve either a single row of vertically elongated areolae *c.* 7·5 μm by 1·5 μm opening into marginal chambers or 2–3 rows, the uppermost somewhat elongated vertically and opening into marginal chambers; at the corners of the valve rather smaller than on the valve face and in horizontal rows, and with a vertical hyaline space at the apex not quite reaching to the summit of the elevation; on the summits of the elevations a few small areolae. Scattered interstrial pores present on the valve face. A ring of very slightly raised linking spines 0·5–1·5 μm apart around the margin of the summit of each elevation. A circular costa 7–40 μm in diameter in the centre of the valve face bearing hollow spines 3–4 μm apart and penetrated by 1–9 labiate processes, and with one costa, or occasionally up to 3, radiating from the ring to the centre of each side of the valve; the circular and radiating costae occasionally absent, but a circular hyaline ring with spines and labiate processes arising from it present. 1–4 labiate processes usually present between the circular costa or hyaline ring and each apex but absent or present towards only one apex in the smaller specimens. The internal opening of each labiate process a straight slit *c.* 2 μm long across an elliptical papilla, the external part a straight cylindrical tube up to 80 μm tall and *c.* 2 μm in diameter. Margin of the valve scarcely thickened and no pseudosepta present.

Palaeocene. Ulyanovsk oblast, U.S.S.R. (Proshkina-Lavrenko et al., 1949).
Anan'ino, Ulyanovsk oblast, U.S.S.R. (BM 52973, 74065).
Arkhangel'skoye-Kuroyedovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams F1417; Witt, 1886; A. Schmidt, 1886*b*).
Smol'kovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams C966).
Ulyanovsk (formerly Simbirsk), Ulyanovsk oblast, U.S.S.R. (BM 52914, 53132).
'Syzran', U.S.S.R. (for this locality see p. 276) (BM 37599, 37600).
Kuibyshev oblast, U.S.S.R (Proshkina-Lavrenko et al. 1949).
Palaeocene–lower Eocene. 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R. (BM SEM 25018–25036).
Upper Eocene. Kuznetsk, Penza oblast, U.S.S.R. (Proshkina-Lavrenko et al., 1949).
Kazakhstan, U.S.S.R. (Sheshukova-Poretskaya & Glezer, 1964).
Upper Eocene to lower Oligocene. Ukraine, U.S.S.R. (Sheshukova-Poretskaya & Glezer, 1964: Glezer et al., 1974).
Upper Miocene. 'Castel' = Szurdokpüspöki, Hungary (BM SEM B35.3–10).

Although it is a variable species, *Trinacria coronata* is distinctive and easily recognizable. The principal variations are in the extent to which the circular and radial costae are developed and in the number of labiate processes present. In some specimens the costae are completely absent, but in these the arrangement of the labiate processes, and the presence of a hyaline ring with spines arising from it in the position where the circular costa occurs when it is present, make identification simple. *Trinacria subcoronata* Sheshukova-Poretskaya & Glezer is based on specimens in which either the radial costae only or the circular one as well are not present. It is reported only from the upper Eocene of Kazakhstan and the upper Eocene to Oligocene of the Ukraine, where specimens with fully developed circular and radial costae have apparently not been found. However, specimens both with and without costae occur in the Palaeocene of the middle Volga basin from the outcrop at Anan'ino (see Fig. 95) and in material labelled 'Syzran'.

There is a considerable but continuous range of size in *Trinacria coronata*, and the smaller specimens differ from the larger in having many fewer labiate processes both in the ring and between it and the apices. There may be none of the latter in the smallest specimens, but more often there is only one between one of the apices and the circular costa. *Trinacria princeps* is based on specimens from the lower part of the size range. Witt (1886) presumably saw only specimens from towards the two extremes of that range and considered that the small ones were specifically distinct from the large ones.

The single specimen from the upper Miocene of Hungary that we have seen differs in various minor respects from the Palaeocene to lower Eocene specimens from the U.S.S.R. The latter have only three radial costae, one running from the circular costa to the centre of each side of the valve, the labiate processes not arising from the circular costa are all approximately on the lines joining the centre of the valve and the apices, there is only a single row of areolae on the mantle, and there are 20 or more minute linking spines surrounding the summits of the elevations. The Hungarian specimen has two or three radial costae running from the circular costa towards each side of the valve, some of them not reaching the margin, its labiate processes not arising from the circular costa are irregularly distributed, it has more than one row of areolae on the mantle, and it has fewer than 10 linking spines on each elevation. These differences are probably such as to justify separation at infraspecific level but we have seen only one specimen with these characteristics and do not feel justified in erecting a new taxon on the basis of it alone.

Strel'nikova (1974) transferred *Trinacria coronata* to *Triceratium* as she considered *Trinacria* to be a synonym of this. However, her figures show that she misapplied the name to a species without the circular costa or hyaline ring bearing spines that is characteristic of this species. The name *Trinacria subcoronata* has always been correctly applied, but this is not the case with *T. princeps*. As we pointed out above (p. 290) Schulz's (1935) record of *T. princeps* from the upper Cretaceous of the Gulf of Danzig is probably based on specimens of *T. interlineata* J. A. Long et al. or *T. fimbriata* P. A. Sims & R. Ross. Hajós & Stradner (1975: 932, pl. 10 figs 7, 8, two figures of the same specimen rotated 120°), when recording *T. princeps* from the upper Cretaceous of the South Pacific Ocean, figured a valve with a high central dome and without the circular and radial costae characteristic of the species or the hyaline ring bearing spines that is present when these are lacking. Glezer et al. (1974: tabl. XIV fig. 5) figure a very similar specimen identified as *T. princeps* from the lower Palaeocene of the middle Volga basin. The correct identity of these two specimens cannot be determined from these illustrations.

We have seen specimens of *Trinacria coronata* from the Palaeocene and perhaps lower Eocene of the middle Volga basin U.S.S.R., and the specimens described and figured by Witt (1886) and A. Schmidt (1886*b*) are from this area and age. Proshkina-Lavrenko et al. (1949: 194) record the species from Ulyanovsk and Kuibyshev oblasts, both in the middle Volga basin. One of their figures of the species (tabl. 74 fig. 4a) is said to be an original drawing of a specimen from the Palaeocene of Kuznetsk, Penza oblast. Glezer, however, (in Glezer et al., 1974: 135) agrees with Deflandre (1950) that the deposit containing diatoms from this locality is upper Eocene in date. It should be noted that the magnification given for this illustration by Proshkina-Lavrenko et al. is incorrect; it is said to be ×1000, but if the figure is to agree with the description given in the work it must be ×500. Fig. 4b, a copy of a figure from A. Schmidt (1886*b*: Taf. 110 fig. 9) of the same species is said to be ×660 but is actually ×425.

Trinacria coronata is thus known to occur in the middle Volga basin in deposits dating from the Palaeocene to the upper Eocene, from the upper Eocene of Kazakhstan and the upper Eocene to lower Oligocene of the Ukraine. The only other record is from the upper Miocene of Hungary, which gives a distribution with a remarkable hiatus.

Discussion

The species described above all possess buttresses at the base of the external tube of their labiate processes, these buttresses in some of the species being extended over the surface of the valve and uniting to form a pattern of costae or, in *T. coronata*, a 'corona'. Apart from the minor differences that separate one species from another, this is the only characteristic that distinguishes them from many of the other species of *Trinacria*, including *T. regina* Heiberg, the type. The close resemblances between *T. caudata* (Witt) P. A. Sims & R. Ross and *T. insipiens* Witt, and between *T. senta* (Witt) P. A. Sims & R. Ross and *Triceratium grevillei* Witt suggest that buttressed labiates may be a character that has evolved, or been lost, more than once, and that it cannot be regarded as a basis for separation at above the level of species.

The information presented here shows that *Trinacria* is closely related to *Hemiaulus* Heiberg *sensu stricto*, i.e. to such species as *H. proteus* Heiberg (see Sims, 1986: figs 54–56), the type species, *H. polymorphus* Grunow, and *H. februatus* Heiberg (see Ross, Sims & Hasle, 1977: figs

10–16). The only consistent differences between the two genera are the shape of the valve, bipolar in *Hemiaulus*, tripolar or multipolar in *Trinacria*, and the absence in *Trinacria* of transverse costae or sulci. If the view that we expressed earlier (Ross, Sims & Hasle, 1977: 194–195), that *Hemiaulus hauckii* Grunow, *H. sinensis* Greville, and *H. membranaceus* Cleve are congeneric with such species as *H. proteus* and *H. polymorphus* is correct, the second of these two differences does not hold consistently. One of us (Sims, 1986) has recently shown that *Sphynctolethus* Hanna, *Ceratulina* H. Peragallo ex Schütt, and *Eucampia* Ehrenb., all genera with a costate ocellus, are closely related to *Hemiaulus*. In this connection, it is interesting to note that the areolae on the summits of the elevations in *Trinacria barronii* P. A. Sims & R. Ross, a Cretaceous species, are in apically directed rows, and in some specimens, but not all, these rows are separated by low ridges (Figs 39, 45). The structure in such specimens thus has the appearance of a poorly developed costate ocellus. This suggests that a tendency to develop in a way that led to the costate ocellus was present in the early common ancestors of the Hemiauloideae.

Sims (1986) has pointed out that *Hemiaulus, Sphynctolethus, Cerataulina, Eucampia, Ailuretta* P. A. Sims, and *Pseudaulacodiscus* Vekshina are a group of closely related genera. As we have pointed out above, *Trinacria* also belongs with them. Re-consideration of the affinities of *Monile* R. Ross & P. A. Sims (1987) leads us to the view that it, too, may be closely related. It differs from *Hemiaulus* in having more than one central labiate process, in having a discrete patch of small areolae on the distal face of each elevation, and in the ring of radial ridges, instead of one or two linking spines, on the summit of its elevations. The patch of small areolae on the elevations, which we treated as a subocellus, can be regarded as an extension of the small areolae found on the summits of the elevations in *Hemiaulus* (see Ross, Sims & Hasle, 1977: figs 16, 47) and *Trinacria* (see Figs 12, 40, 46, 56, 67, 75); the ring of radial ridges is very similar to the reduced linking spines of *T. coronata* (compare Ross & Sims, 1987: figs 63, 64 with Fig. 75 of this paper). These eight genera are all that we would currently include in the subfamily Hemiauloideae of the Biddulphiaceae. The many genera of the Biddulphiaceae with interlocking linking spines that we have previously surveyed (Ross & Sims, 1985, 1987) differ to such an extent in other respects from those we include in the Hemiauloideae as to exclude them from this subfamily. The one possible exception is *Dextradonator* R. Ross & P. A. Sims (1980), but that has so many features peculiar to itself that its relationship to other genera is obscure. It may well be a resting spore.

Of the quadripolar taxa considered here, *Trinacria barronii* forma *tetragona* appears earliest in the fossil record, near the top of the Maastrichtian. Some specimens of it have a vertical hyaline space at the apex, others do not. It is simple, but perhaps over-simplifying, to postulate that marginal chambers began to develop in its descendants, and that divergence between forms without and with a vertical hyaline space took place before they were fully developed. In those without a vertical hyaline space the number of labiate processes was reduced to one, giving *T. ecostata*. In the other group the marginal chambers became fully developed and the hyaline space at the apex developed into a costa, whilst the number of labiate processes continued to be variable, with the range coming to include one as well as two to four. This resulted in *T. cornuta*, and the transition from that to *T. cristata*, differentiated only by the radiating folds of its valve face and the fact that its labiate process is always single and central, can readily be envisaged. The arrangement of the linking spines provides further evidence for the close relationship of these four species: in all of them one of each pair of sibling valves has two large linking spines continuing the marginal ridges, the other a single large linking spine in the centre of the proximal side of the summit of the elevations, and the distal linking spines, if any are present, are much smaller. *T. barronii* forma *barronii* is the only one of the tripolar taxa considered here to have such an arrangement.

The pattern of similarities between the tripolar taxa is much more complex. *Trinacria interlineata* and *T. fimbriata*, both upper Cretaceous species, are obviously closely related and it is not difficult to suppose that the pattern of costae and labiate processes found in *T. coronata*, first recorded in the Palaeocene, evolved from that found in these two species. However, *T. coronata* has a fimbriate marginal ridge, as has *T. fimbriata* but not *T. interlineata*, but the

elevations of *T. fimbriata* are very small at the summit with only one large linking spine, those of *T. interlineata* are larger, with a ring of 6–10 linking spines, the two proximal ones larger than the others, whilst *T. coronata* has even larger summits to its elevations, each with up to 20 small linking spines of even size. *T. coronata* has marginal chambers, not present in *T. interlineata* or *T. fimbriata* but found in *T. senta* and *T. caudata*, species in which the buttresses of the labiate processes do not unite to form a definite pattern of costae, and in the quadripolar *T. cornuta*, which, like *T. coronata* but no other tripolar species, has vertical costae at the apices. *T. cancellata*, first recorded from the upper Campanian, has secondary pseudosepta, as has *T. caudata*, first recorded in the Palaeocene, and there seems no difficulty in supposing an evolutionary transition from the three labiate processes penetrating a triradiate pattern of costae found in *T. cancellata* to the single buttressed labiate process of *T. caudata*. However, *T. cancellata* has no linking spines, a character probably derived by loss rather than primitive, whilst these are present in *T. caudata*. Also, in *T. cancellata* internal costae along the margins are separated laterally by more than one areola and project further into the frustule than the walls of the marginal chambers of *T. caudata*, which are only one areola wide. Some, at least, of these characters, presence of marginal chambers, buttresses of labiate processes united to form external costae, secondary pseudosepta, a vertical costa at the apex, fimbriate margins, must be polyphyletic, but with the information currently available to us we cannot tell which.

The distribution patterns of some of the species considered here have unusual features. Of the species with records in the Cretaceous, *T. fimbriata* is known only from California and *T. barronii* only from the Alpha Ridge in the Arctic Ocean, whilst *T. interlineata* was more widespread, occurring in the south-west Pacific Ocean, at Seymour Island off the Antarctic Peninsula, and in California. *T. interlineata*, and possibly also *T. barronii*, survived into the lowermost Palaeocene but there are no later records. The other two species known from the Cretaceous. *T. cancellata* and *T. senta*, were much longer lived, persisting until the upper Eocene, perhaps later, and the lower Miocene respectively. Of the other species, *T. ecostata* is known only from the Palaeocene and possibly lower Eocene of the middle Volga basin of the U.S.S.R. and *T. cristata* only from the lower Eocene of the north-west Atlantic and from one outcrop of uncertain age of the middle Eocene to lower Miocene Oceanic Beds of Barbados. *T. cornuta*, recorded from the Palaeocene of the Indian Ocean and the Cape basin of the South Atlantic Ocean, has an Eocene distribution similar to that of *T. cancellata*. Both occurred in the lower Eocene of Denmark, in the lower to the upper Eocene of west Siberia, in the upper Eocene of the middle Volga basin, in the middle Eocene to lower Miocene Oceanic Beds of Barbados, and in the middle Eocene of the south-western part of the North Atlantic Ocean. This last is the only Eocene record of *T. cancellata* from the Atlantic Ocean, but there are other Eocene records of *T. cornuta* from that ocean. *T. caudata*, known only from the Palaeocene of the middle Volga basin and the Miocene of the Caribbean and California has a remarkable hiatus in its known distribution. *T. coronata*, another species with its earliest occurrence in the Palaeocene of the middle Volga basin, also survived into the Miocene but its geographical distribution was more limited; its other records are from the upper Eocene of the middle Volga basin, Kazakhstan and the Ukraine, and from the upper Miocene of Hungary.

Four of the species discussed here, *T. ecostata, T. senta, T. caudata*, and *T. coronata*, occur in the Palaeocene of the middle Volga basin. It is interesting that only one of them, *T. senta*, is recorded from the Palaeocene and lower Eocene deposits of western Siberia. Only one of them, *T. coronata*, is recorded from the upper Eocene of the middle Volga basin, along with both the species present in the lower Eocene of west Siberia but not recorded from the Palaeocene of the middle Volga basin.

Five of the species dealt with in this paper occurred in the upper Cretaceous. There is no later record of one of them, *Trinacria fimbriata*. The species *T. interlineata* survived into the lower Palaeocene (Harwood, 1988), and *T. barronii* probably did so; it is present in the upper as well as the lower parts of CESAR core 6 and FI-437 (see p. 277 above). *T. cancellata* and *T. senta* persisted from the upper Cretaceous to at least the upper Eocene and the lower Miocene respectively. Kitchell et al. (1986) have recently suggested that many species of diatoms were able to survive through the Cretaceous to Palaeocene transition, when so many planktonic

organisms became extinct, because they produced resting spores. Although resting spores are well known in *Hemiaulus* and some other members of the Hemiauloideae, none have been reported in *Trinacria*. However, *T. simulacrum* Grove & Sturt (1887*b*), recorded from the Palaeocene (Gombos, 1977, 1984) to the Oligocene (Gombos, 1977), and *T. ventricosa* Grove & Sturt (1887*a*), recorded from the upper Eocene and Oligocene (Proshkina-Lavrenko et al., 1949), have characteristics which suggest that they might be resting spores, as have some other members of the genus, but there is no record of any of these being found associated with what might be vegetative valves. It must therefore remain doubtful whether any species of *Trinacria* produced resting sporses.

It is also of interest that *Trinacria caudata* and *T. coronata* both survived the mass extinction between the Oligocene and the Miocene, and *T. senta* may have done so also, although the lower Miocene dating of the fossil diatoms from Jérémie, Haiti, is perhaps too late (see Ross & Sims, 1985: 284).

According to Proshkina-Lavrenko (1974; in Glezer et al., 1974: 45–49) the structure of the areolae is the basis on which the centric diatoms should be separated into orders, as the various types of areolae must be regarded as monophylectic. In this she has been followed by Glezer (1979, 1986), who restricts the order Biddulphiales to genera with poroid areolae, and includes all those with loculate areolae in which the vela are external and the foramina internal in the Coscinodiscales. The resemblances between genera that she places one in one family, one in the other, she attributes to convergence and parallelism. Both we (Ross & Sims, 1973) and Simonsen (1979), however, when considering how the system of classification of centric diatoms should be revised in the light of observations made with the transmission and scanning electron microscopes, have postulated that the transition from poroid to loculate areolae has arisen more than once. In *Trinacria coronata*, a species so closely resembling the others described above, the areolae are slightly constricted at their inner opening so that this has a diameter only about ⅘ of their external opening. This shows that there is at least a tendency in *Trinacria* for loculate areolae to be developed from poroid ones.

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Description of plates

Plate 1. *Trinacria cornuta* (Grev.) P. A. Sims & R. Ross. Figs 1–4, 7–9: 'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.; Figs 5–6, 9: south-western Atlantic, Falkland Plateau, 51° 08′ S, 54° 22′ W, 2880 m depth; Vema cruise 17, core 107, 50 cm (Fig. 9) and 120 cm (Figs 5–6). Figs 1, 2, 6, 7, 9: bar line = 10 μm; Figs 3–5, 8: bar line = 3 μm.

Fig. 1: two valves linked by spines at the summits of their elevations. A hyaline marginal ridge is continuous between the summits of the elevations and a hyaline ridge or costa (arrow) extends from the valve margin to each summit. Fig. 2: a single frustule in girdle view with a cingulum of at least three closed bands to each valve. Fig. 3: oblique view showing domed valve face with buttressed labiate process, cribra and interstrial pores (arrows). *N.B.* Mantle areolae larger than those on the valve face and elevations. Fig. 4: summit of elevation with two large linking spines continuing the marginal ridges and smaller ones on the distal edges of the summit. Note slot into which the large spine of the opposing valve fits, also areolae on summit. Fig. 5: oblique view showing the fine tubular extension of the labiate process with buttresses at its base, also cribra and interstrial pores with external rims projecting as hollow spines (arrowheads). Fig. 6: oblique view of valve exterior showing well-developed marginal ridge extending between the summits of 4 slender elevations and also the vertical costae at the apices. Fig. 7: interior view of quadripolar valve displaying concave valve margins with small pseudosepta at acuminate apices, also upper row of mantle areolae and outer row of valve areolae opening into marginal chambers (arrows). Note also internal opening from labiate process (arrowhead). Fig. 8: detail of girdle bands. Fig. 9: forma *pentagona* P. A. Sims & R. Ross; five-angled valve showing hyaline central area, off-centre labiate process, also hyaline vertical ridge on distal face of elevation.

Plate 2. *Trinacria ecostata* P. A. Sims & R. Ross. Figs 10–13: 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R.; Figs 14–15: Simbirsk (now Ulyanovsk), Ulyanovsk oblast, U.S.S.R. Figs 10, 11, 14: bar line = 20 μm; Figs 12, 13, 15: bar line = 3 μm.

Fig. 10: oblique view of valve exterior with vertical mantle and a well-developed marginal ridge continuous between the summits of the four elevations but no vertical costae at apices. Fig. 11: valve lying flat, exterior view showing concave valve margins and single off-centre labiate process. Fig. 12: elevation with rows of small areolae on summit, also one of the two large linking spines continuing the marginal ridges and four small linking spines. Fig. 13: oblique view showing external tube from labiate process buttressed at its base, cribra occluding areolae, and interstrial pores. Fig. 14: oblique view of valve interior with opening from single labiate process, pseudosepta (arrowhead) at narrow rounded apices, and small internal costae between outer row of areolae on valve face and upper row on mantle (arrows). Fig. 15: valve interior with cribra and inner opening of labiate process.

Plate 3. *Trinacria cancellata* (Grev.) P. A. Sims & R. Ross. Figs 16–17, 22–23: Barbados; Figs 18–21: Njkjøbing, Island of Mors, Denmark. Figs 16–18, 22: bar line = 20 μm; Figs 19–21, 23: bar line = 3 μm.

Fig. 16: valve with straight sides, narrowly rounded apices, a shallowly domed valve face and two linked

labiate processes at centre. Fig. 17: valve with straight sides and produced subcapitate apices. Valve face almost flat and elevations barely raised. Fig. 18: valve with slightly concave sides, weakly produced apices, three linked labiate processes, and a marginal ridge continuous between the summits of the three elevations. Figs 19: tubular openings from three labiate processes linked by external costae (buttresses) to form a triradiate pattern. Fig. 20: summit of elevation with short blunt spines between the three rows of areolae. Summit surrounded by a low hyaline ridge on its outer margin. Fig. 21: triradiate pattern of costae with two labiate processes and a solid spine broken off. Fig. 22: oblique view of valve interior with well-developed pseudosepta at apices and costae projecting internally from vertical mantle (arrows). Fig. 23: interior openings from labiate processes, and internal costae projecting from mantle and valve margin.

Plate 4. *Trinacria interlineata* J. A. Long et al. Figs 24–30: Moreno Shale, Moreno Gulch, Fresno County, California, U.S.A. Figs 24, 25, 29: bar line = 10 μm; Figs 26–28, 30: bar line = 3 μm.

Fig. 24: valve exterior, tilted 45°, with shallowly domed valve face separated from elevations by deep depressions. Elevations tapering from base to summit with a well-developed hyaline marginal ridge continuous between summits. Note vertical mantle with deep indentation opposite depressions of valve face. Fig. 25: valve, triangular in outline, with domed valve face separated from apices by depressions, constricted on each side by an indentation of the mantle. Radiating from valve centre are three strong costae which extend to the valve margin and between each pair is a weaker costa. Fig. 26: oblique view with three strong costae fusing at valve centre with a weaker costa between each pair. About ⅓ to ½ way (⅔ on weaker costae) along each costa is a long tubular projection, the external opening from a labiate process. Fig. 27: valve mantle separated from valve face by the hyaline marginal ridge. Areolae with vela in the form of rotae, those on the mantle larger than those on the valve face; interstrial pores also present. Fig. 28: proximal face of elevation with 8 linking spines positioned around a subcircular flattened summit. Fig. 29: valve interior with small pseudosepta at apices and hyaline rays beneath external costae. Fig. 30: valve centre, with internal openings from four labiate processes positioned beneath external costae.

Plate 5. *Trinacria fimbriata* P. A. Sims & R. Ross. Figs 31–36: Moreno Shale, Moreno Gulch, Fresno County, California, U.S.A. Figs 31–32: bar line = 10 μm; Figs 33–36: bar line = 5 μm.

Fig. 31: valve exterior tilted 45°, with three elevations, each with a single spine at its summit, a domed valve face and a well-developed marginal ridge continuous between the summits and bearing spines along the valve margin. Note valve mantle raised at centre. Fig. 32: same valve, flat, displaying hexagonal valve face separated from the elevations by deep depressions. Fig. 33: hexagonal valve face with three deep costae radiating from the valve centre to each margin, also six less well-developed costae, two in each segment. Extending from each costa, at approximately half-way is the long tubular opening of a labiate process. Fig. 34: elevation with a single spine at its summit. Note flattened spines arising from marginal ridge, and hyaline ridge on distal side of elevation (arrow). Fig. 35: valve centre showing depth of radiating costae, also the tubular projections of the labiate processes. Fig. 36: elevation with areolae on flattened summit and a single beaked linking spine, the extension from a marginal ridge.

Plate 6. *Trinacria barronii* forma *barronii* P. A. Sims & R. Ross. Figs 37–40: Alpha Ridge, Arctic Ocean, 85° 59·87′ N, 129° 58·76′ W, 1584 m depth. U.S.G.S. site F1-437-15C; Figs 41–43: Alpha Ridge, Arctic Ocean, 85° 50′ 0·41″ N, 109° 01′ 0·52″ W, 1365 m depth. CESAR core 6; Figs 41, 42: D9, 270–272; Fig. 43: D4, 170–172. Figs 37, 41, 43: bar line = 10 μm; Figs 38–40, 42: bar line = 3 μm.

Fig. 37: oblique view of valve with weakly domed valve face, a vertical mantle and three elevations with flattened summits each with a single spine on its proximal face. Between the summits of the elevations is a well-developed marginal ridge. Fig. 38: thick tubular extension from one (of two) labiate process with many buttresses at its base, also areolae with cribra and scattered interstrial pores with raised rims. Fig. 39: elevation with two linking spines, each the continuation of a marginal ridge. Note flattened summits with three rows of small areolae separated by low ridges. Fig. 40: elevation with a single spine on its proximal face and a flattened summit with rows of small areolae. Note small spines around margin of summit. Fig. 41: valve exterior with slightly convex sides and produced rounded apices. Fig. 42: detail of tubular extensions from two labiate processes, each with two thick buttresses. Fig. 43: oblique view of valve interior with valve margin extended into small pseudosepta at apices, also marginal chambers into which the outer row of valve areolae and upper row of mantle areolae open (arrows).

Plate 7. *Trinacria barronii* forma *tetragona* P. A. Sims & R. Ross. Figs 44–48. Figs 44, 45, 48; Alpha Ridge, Arctic Ocean, 85° 59·87′ N, 129° 58·76′ W, 1584 m depth; U.S.G.S. site F1-437-15C; Figs 46–47: Alpha Ridge, Arctic Ocean, 85° 50′ 0·41″ N, 109° 01′ 0·52″ W, 1365 m depth; CESAR core 6, D4, 170–172. Figs 44–45, 47, 49–50: bar line = 10 μm; Figs 46, 48: bar line = 3 μm.

Fig. 44: quadripolar valve with concave margins and produced rounded apices; diagonals unequal. Three labiate processes are positioned near the valve margins. Fig. 45: oblique view of same valve showing vertical mantle and a well-developed marginal ridge continuous between the summits of the elevations. Fig. 46: detail of summit with single large linking spine extending from proximal face of elevation and three

rows of small areolae interspersed with papillae. Note also small spines on margin of summit (arrows). Fig. 47: interior view of valve with attached girdle bands. Note opening from labiate process, also pseudosepta at apices. Fig. 48: detail of valve interior with cribra occluding areolae, interstrial pores, marginal chambers and slit-like opening from a labiate process.

Trinacria indefinita Jousé. Fig. 49: Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. Bar line = 10 μm. Valve exterior with convex valve margins and three produced and rounded apices. Elevations broad with flattened summits surrounded by linking spines. Marginal ridge continuous between summits. Note opening from off-centre labiate process not buttressed.

Trinacria acutangula Barron. Fig. 50: Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. Bar line = 10 μm. Valve margin weakly concave between three acute apices. Elevations narrow, with linking spines and small areolae on summits and marginal ridge continuous between summits of elevations. Areolae with finely perforate cribra, and a single labiate process without buttresses.

Plate 8. *Trinacria senta* (Witt) P. A. Sims & R. Ross. Figs 51–52: 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R. Figs 53, 55: Falkland Plateau, south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 102 cm; Figs 54, 56: Simbirsk (now Ulyanovsk), Ulyanovsk oblast, U.S.S.R. Figs 51, 53, 54: bar line = 20 μm; Figs 52, 55, 56: bar line = 5 μm.

Fig. 51: valve exterior of tripolar valve with slightly concave sides and acutely rounded apices. Areolae in radial rows, and tubular openings from five labiate processes, each with three or four costae or buttresses, scattered over valve face. Fig. 52: detail of valve face with tubular extensions from labiate processes buttressed by three costae, areolae in radial rows, and scattered interstrial pores with raised rims. Fig. 53: valve exterior tilted 45° with domed valve face, vertical mantle and well-defined marginal ridge continuous between the summits of three elevations. Fig. 54: valve exterior tilted 45° showing variation in number of labiate processes and in the length of their buttresses. Note also marginal chambers (arrows) produced by the outer row of valve areolae and the upper row of mantle areolae. Fig. 55: detail of valve face (Fig. 53) with tubular extensions from 13 labiate processes and buttresses (or costae) anastomosing. Fig. 56: elevation with summit surrounded by small triangular linking spines. Note small areola on summit, marginal ridge extending to the summit of the elevation, and the long tubular projection of a labiate process buttressed at its base.

Plate 9. *Trinacria senta* (Witt) P. A. Sims & R. Ross. Figs 57–58: 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R. Figs 59–60: Simbirsk (now Ulyanovsk), Ulyanovsk oblast, U.S.S.R.; Figs 61–62: Falkland Plateau, south-western Atlantic, 51° 40′ S, 48° 29′ W, 2429 m depth. Vema cruise 18, core 112, 100 cm. Figs 57, 59, 61: bar line = 20 μm; Figs 58, 60, 62: bar line = 5 μm.

Fig. 57: valve exterior tilted 45° showing variation in structure of labiate processes. Here three processes with broad bases are present but the length of the buttresses is abbreviated. Fig. 58: elevation with summit surrounded by seven triangular spines. Note upper row of mantle areolae forming marginal chambers and valve margin projecting beyond mantle. Fig. 59: exterior view of domed valve with three small and barely raised elevations. Note scattered labiate processes barely buttressed at base. Fig. 60: detail at valve centre showing areolae with cribra, interstrial pores, and labiate processes with short buttresses. Fig. 61: valve interior with hyaline valve margin forming pseudosepta at apices, also marginal chambers. Fig. 62: detail at valve centre, interior view showing slit-like openings of labiate processes.

Plate 10. *Trinacria caudata* (Witt) P. A. Sims & R. Ross. Figs 63–68, 70: 'Isenski an der Wolga' (presumed to be Isheyevka, Ulyanovsk oblast), U.S.S.R. Fig. 69: Simbirsk (now Ulyanovsk), Ulyanovsk oblast, U.S.S.R. Figs 63, 65, 66, 68, 70: bar line = 10 μm; Figs 64, 67, 69: bar line = 3 μm.

Fig. 63: tripolar valve with slightly concave sides, narrowly rounded apices and a single off-centre labiate process. Fig. 64: valve exterior with buttressed base of labiate process (arrowhead), areolae with cribra, and interstrial pores with raised rims. Fig. 65: exterior of triangular valve with domed face and flattened summits to the elevations. Fig. 66: valve exterior (as Fig. 65) tilted 45° with marginal ridge continuous between summits of barely raised elevations and a single buttressed labiate process. Fig. 67: elevation with flat summit pierced by three small areolae and encircled by eight triangular spines. Fig. 68: oblique view of valve showing summits of elevations surrounded by small linking spines, a single labiate process positioned towards the valve margin, and vertical mantle. Fig. 69: valve interior with slit-like opening from a single labiate process. Fig. 70: valve interior displaying marginal chambers and pseudosepta at apices.

Plate 11. *Trinacria coronata* Witt. Figs 71–77: 'Carlovo' (presumed to be Karlovka, Kuibyshev oblast), U.S.S.R. Figs 71, 73, 77: bar line = 30 μm; Figs 72, 74, 76: bar line = 10 μm; Fig. 75: bar line = 3 μm.

Fig. 71: valve exterior tilted 45° showing shallowly domed valve face with slightly depressed circular area at centre, three elevations with a hyaline marginal ridge extending between them and bearing spines along the valve margin. Fig. 72: detail at pole showing hyaline marginal ridge with spines, slightly concave mantle with single row of elongate areolae, the long tubular extensions from four labiate processes, and an elevation tapering upwards with a hyaline ridge on its distal side extending from the valve margin almost to

its summit. Fig. 73: valve exterior, lying flat, with slightly concave sides and subacute apices. At valve centre, a circular costa present from which three costae radiate, one to each side. Fig. 74: valve centre with circular costa bearing hollow spines and the long tubular extensions from 7 labiate processes. Note areolae occluded by cribra, and interstrial pores. Fig. 75: summit of elevation with few small areolae encircled by radially aligned and slightly raised linking spines (eroded on this specimen). Fig. 76: valve interior at centre with slit-like openings from labiate processes, areolae with cribra, and interstrial pores. Fig. 77: valve interior showing hyaline areas beneath external costae, also marginal chambers.

Plate 12. Fig. 78: *Trinacria cornuta* forma *cornuta* (Grev.) P. A. Sims & R. Ross, BM coll. Adams J3017: Mors, Jutland, Denmark: full length one side = 40 μm, two linked valves 33 × 43 μm.
Fig. 79: *Trinacria cornuta* forma *pentagona* P. A. Sims & R. Ross, holotype, BM 81486: Falkland Plateau, South Atlantic Ocean, 47° 45·7′ S, 57° 38·5′ W, 3650 m depth; Conrad cuise 12, core 237: valve, 46 μm diameter. Fig. 80: *Trinacria ecostata* P. A. Sims & R. Ross, holotype, BM coll. Adams C960: Smol'kovo, Simbirsk, U.S.S.R.: full length one side = 82 μm. Figs 81–83: *Trinacria cristata* Gombos; Fig. 81: BM coll. Adams F1260: Mt. Hillaby, Barbados: length one side approx. = 35 μm. Fig. 82: BM coll. Adams H245 (Tempère): Mt. Hillaby, Barbados: length one side = 34 μm. Fig. 83: BM coll. Adams GC2741 (Tempère no. 702): Mt Hillaby, Barbados: length one side = 50 μm; note folds in valve face (arrows). Fig. 84: *Trinacria cancellata* (Grev.) P. A. Sims & R. Ross, BM 34291: Fur Island, Jutland, Denmark: valve, 70 × 22 μm; note secondary pseudosepta (arrows). Figs 85–86: *Trinacria interlineata* J. A. Long et al., BM 81432: Moreno, California, U.S.A.: length = 53 μm. Figs 87–88: *Trinacria fimbriata* P. A. Sims & R. Ross, holotype, BM 81427: Moreno, California, U.S.A.: single valve at different focal planes, full length one side = 73 μm.

Plate 13. Fig. 89: *Trinacria barronii* forma *barronii* P. A. Sims & R. Ross, holotype, BM 81428: Alpha Ridge, Arctic Ocean, 85° 50′ 0·41″ N, 109° 01′ 0·52″ W, 1365 m depth; CESAR core 6, D8 250–252 cm: length one side = 33 μm. Fig. 90: *Trinacria barronii* forma *tetragona* P. A. Sims & R. Ross, holotype, BM 81429: Alpha Ridge, Arctic Ocean, 85° 50′ 0·41″ N, 109° 01′ 0·52″ W, 1365 m depth: CESAR core 6, D4 170–172 cm: valve 50 × 40 μm. Figs 91–92: *Trinacria senta* (Witt) P. A. Sims & R. Ross, BM 52962 (Tempère): Simbirsk, U.S.S.R.; Fig. 91: length one side = 112 μm. Fig. 92: valve 100 × 35 μm. Figs 93–94: *Trinacria caudata* (Witt) P. A. Sims & R. Ross, BM 63486 (Thum): Simbirsk, U.S.S.R.; Fig. 93: length one side = 79 μm. Fig. 94: valve 68 × 20 μm; note secondary pseudosepta (arrows). Figs 95–96: *Trinacria coronata* Witt, BM 52973 (Thum): Anan'ino, Simbirsk, U.S.S.R.; Fig. 95: full length one side = 120 μm, N.B. without corona. Fig. 96: full length one side 132 μm.

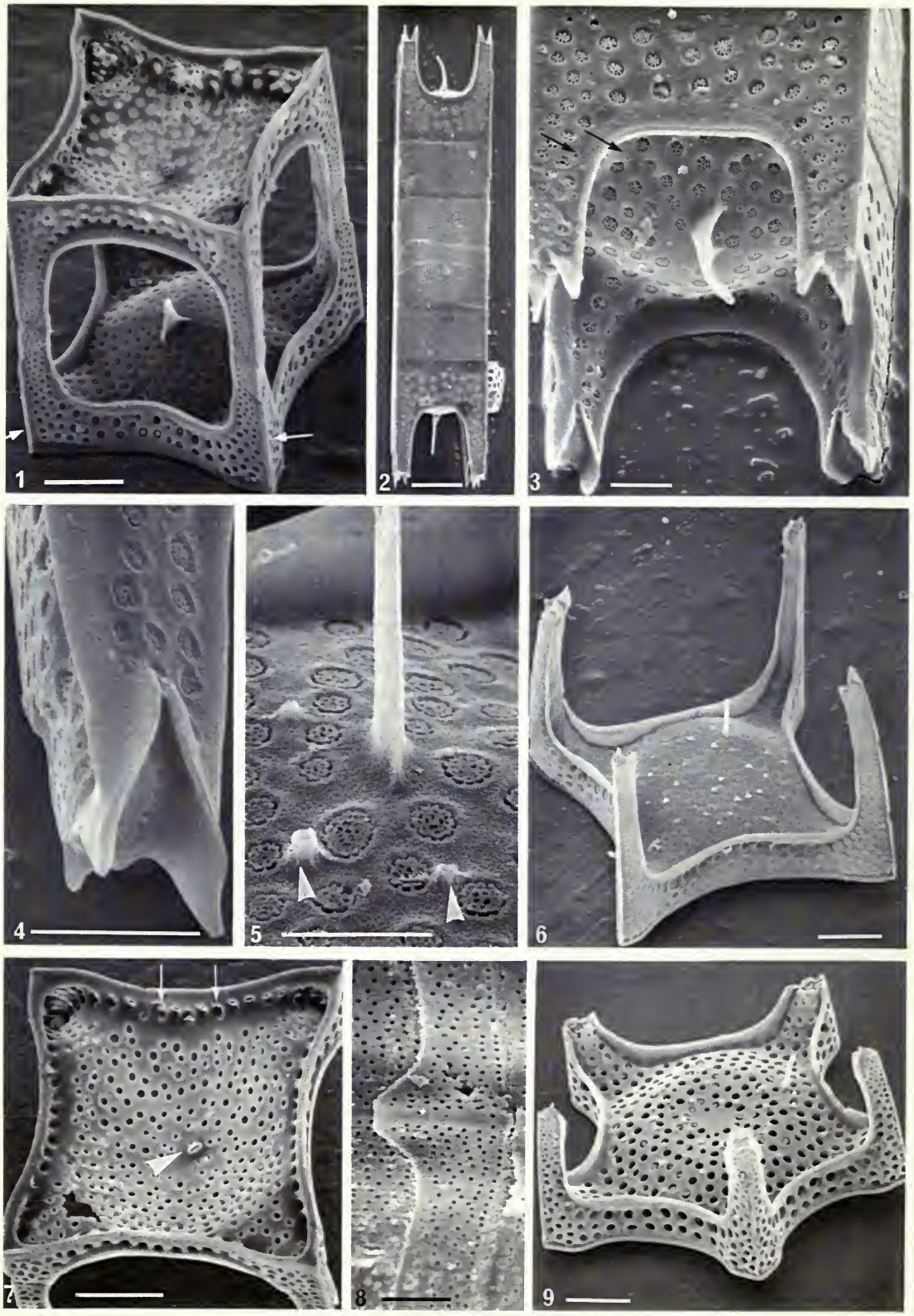
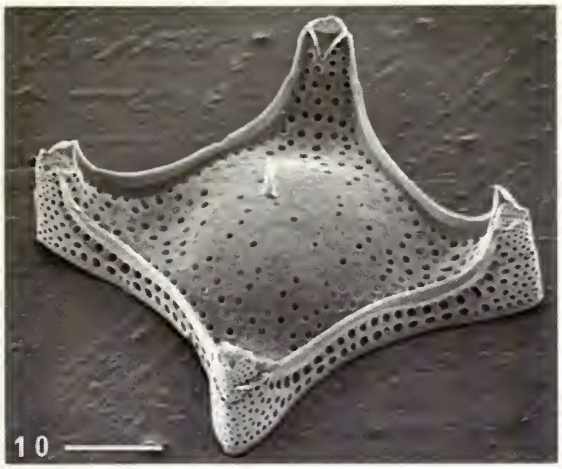
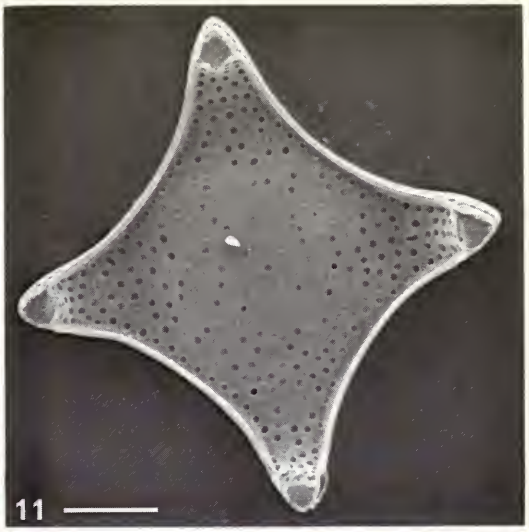
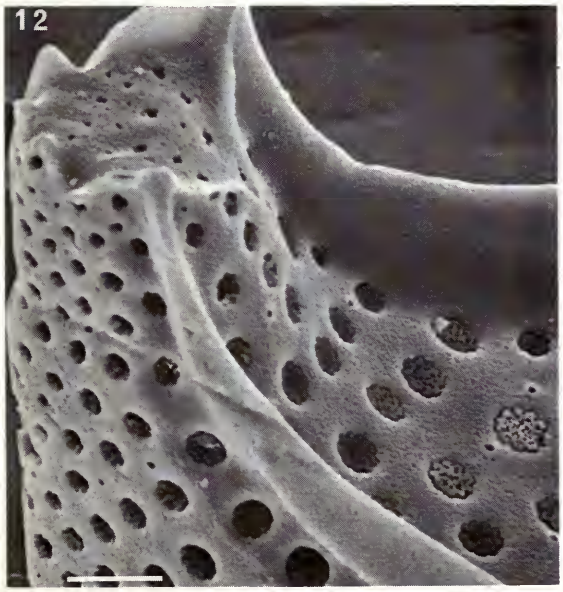
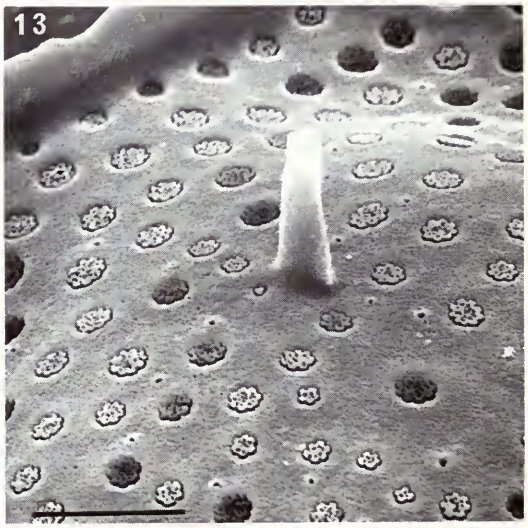


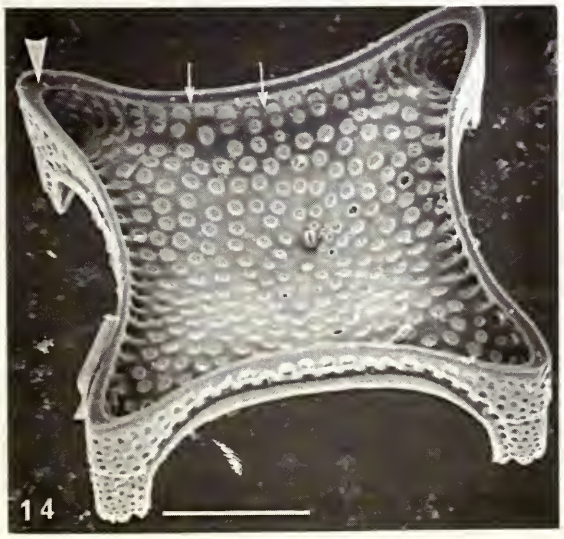
Plate 1

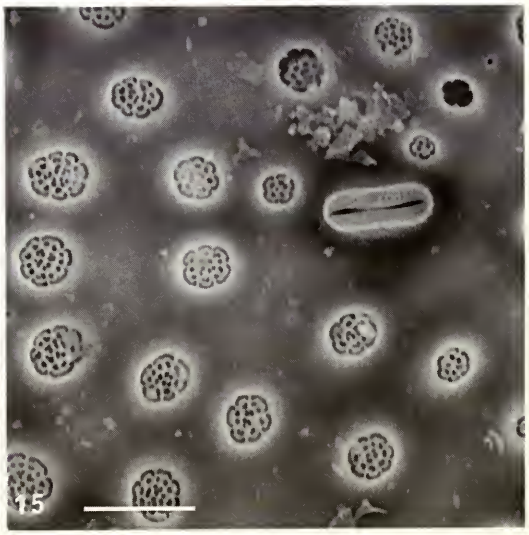












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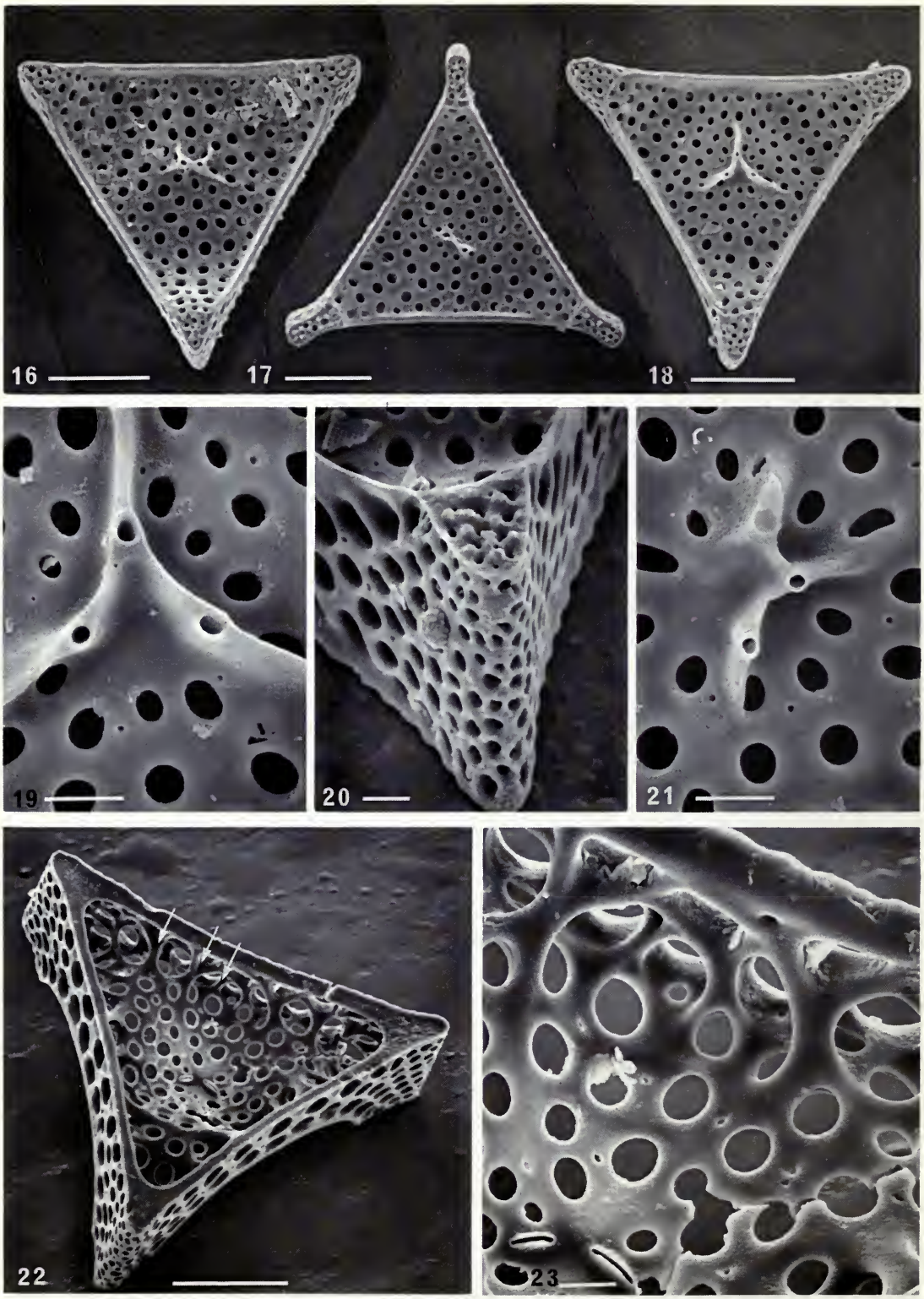

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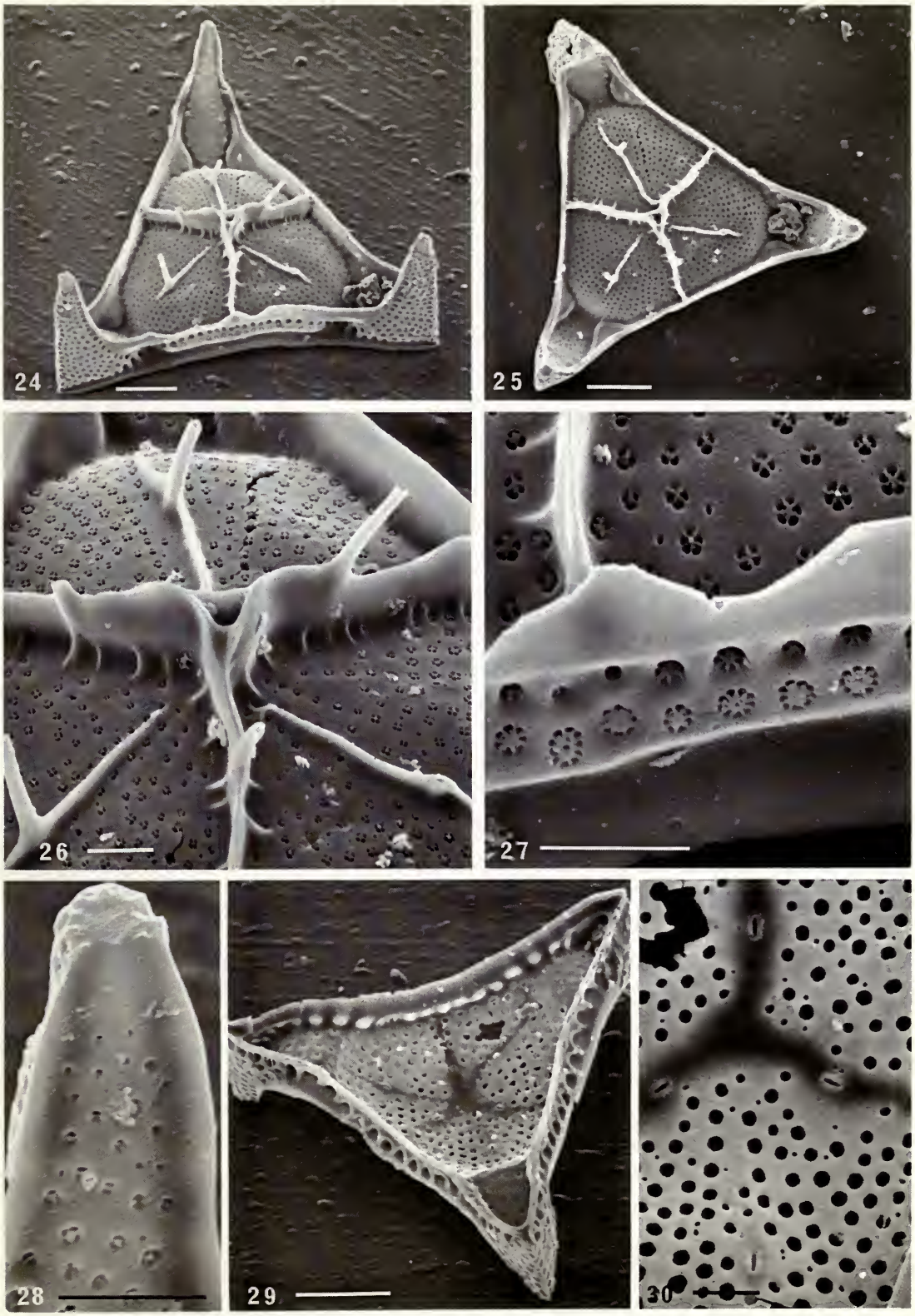

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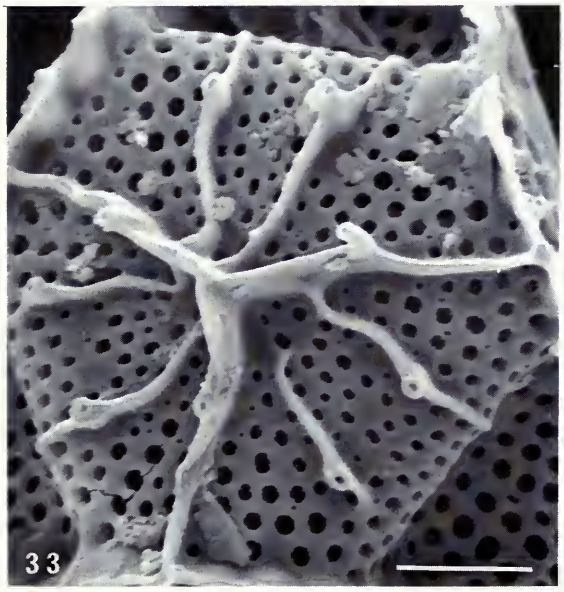

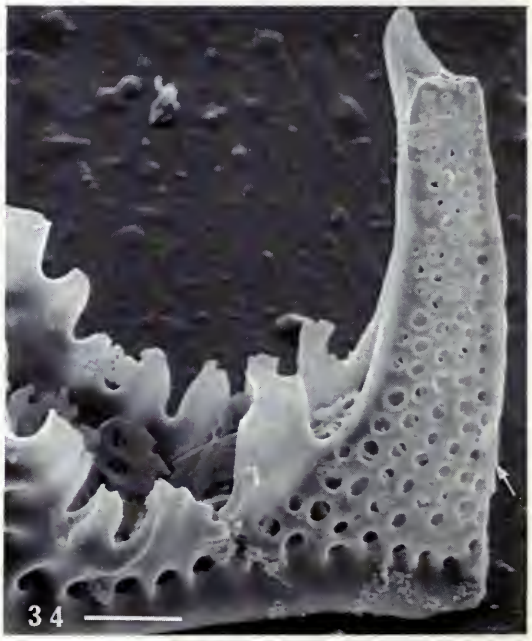

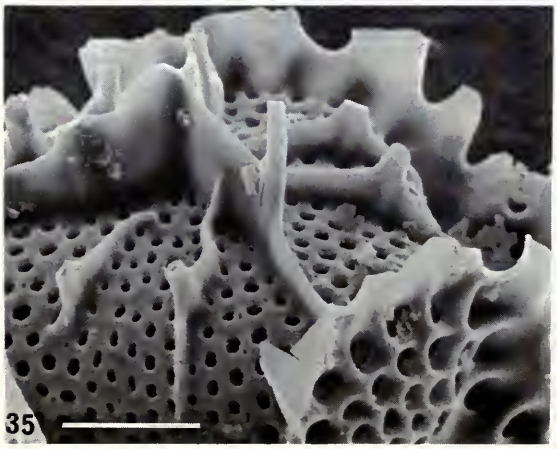

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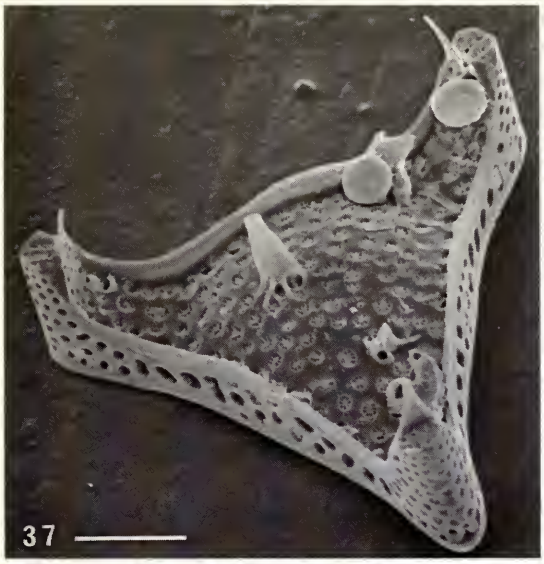

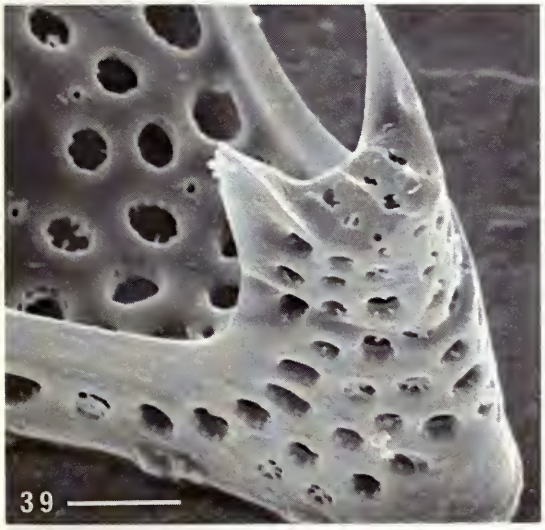

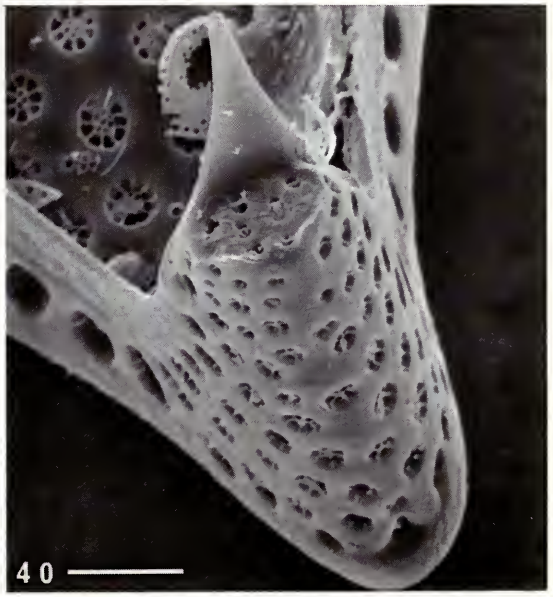

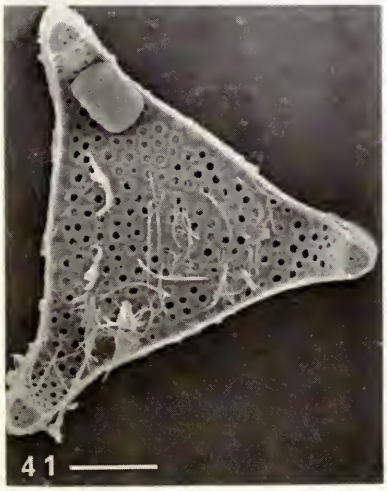

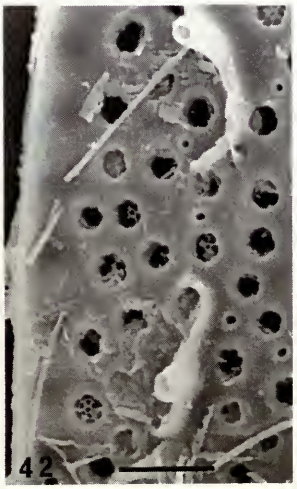

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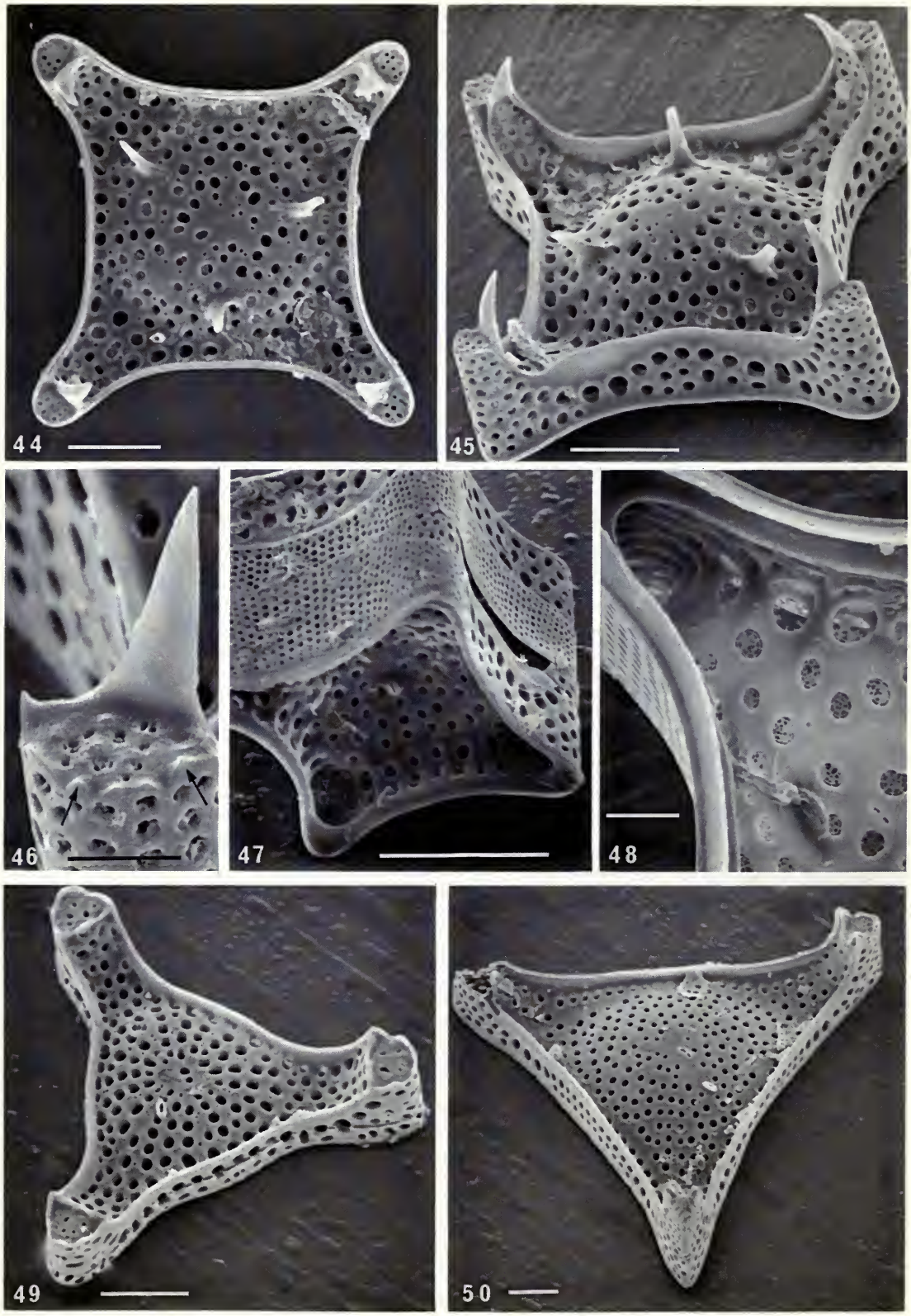

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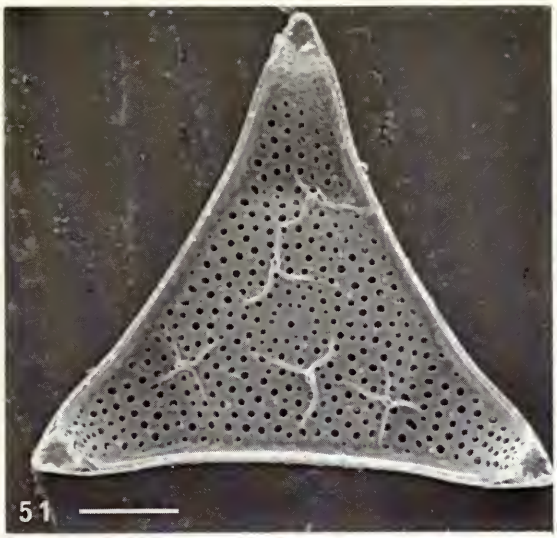

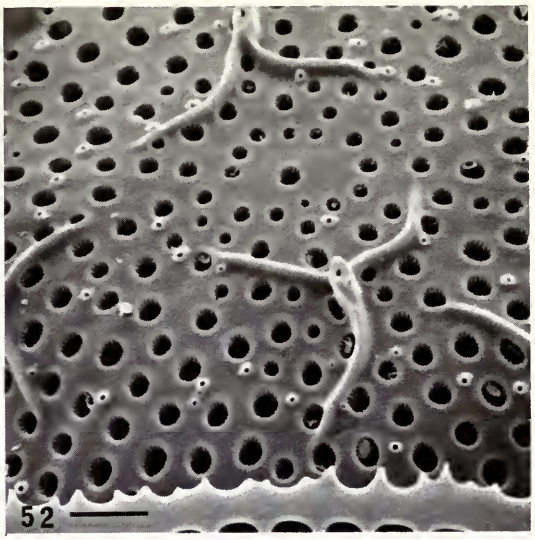

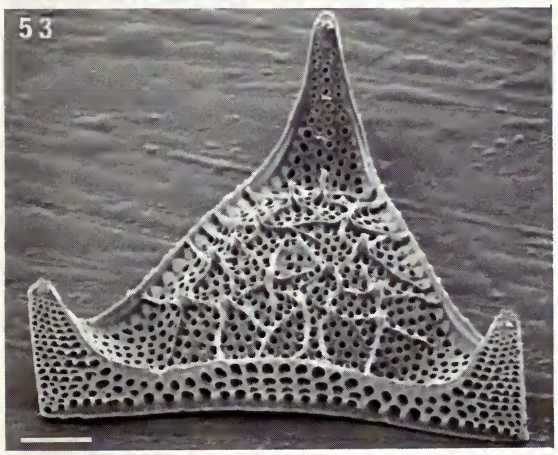

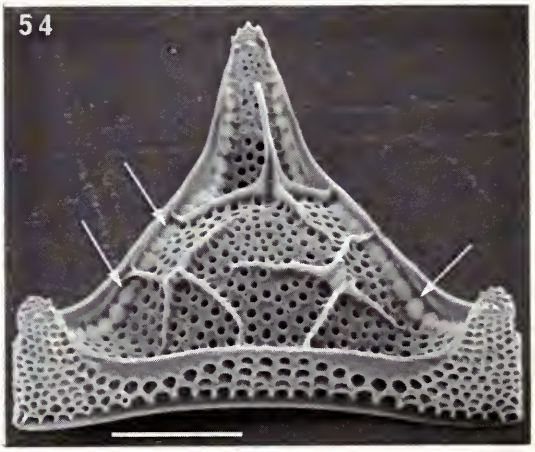

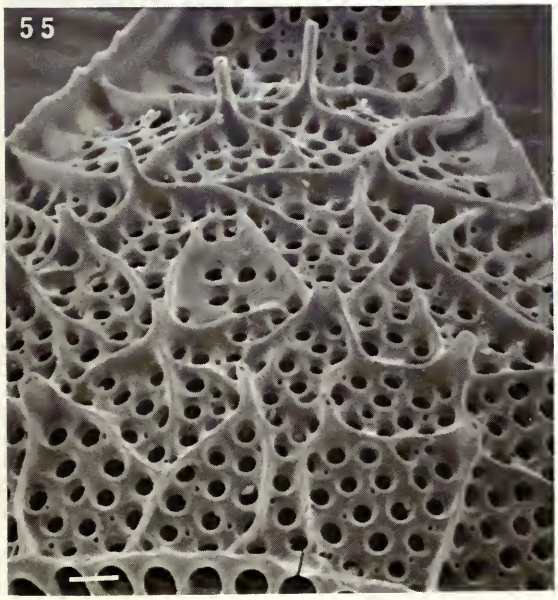

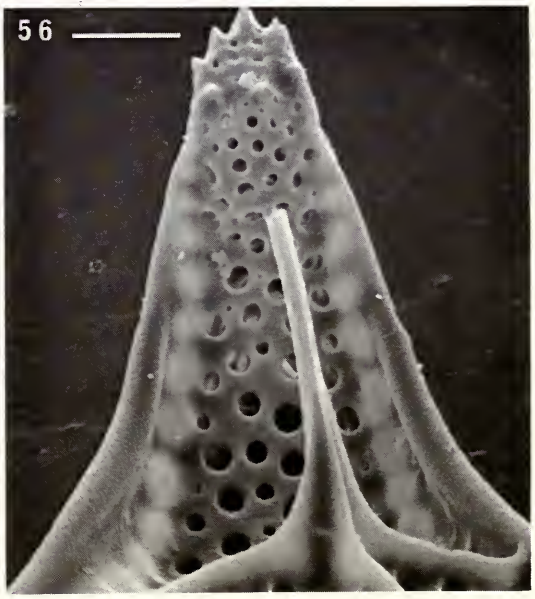

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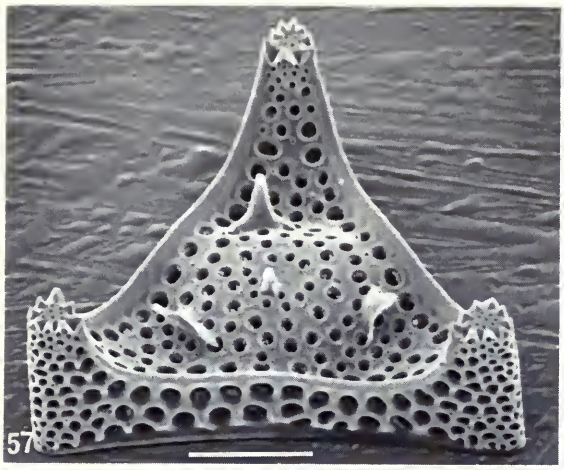

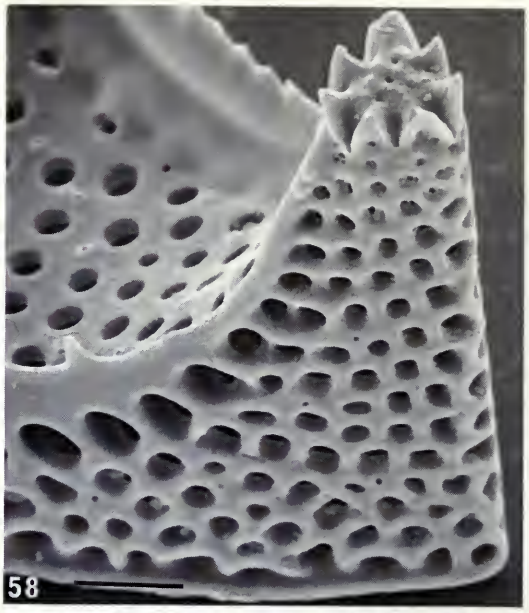

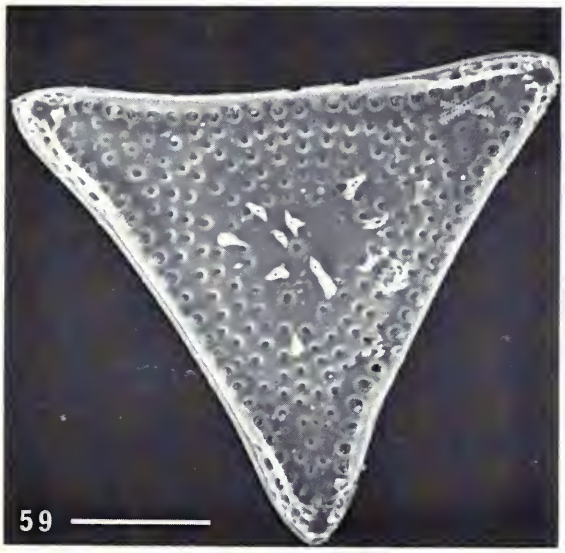

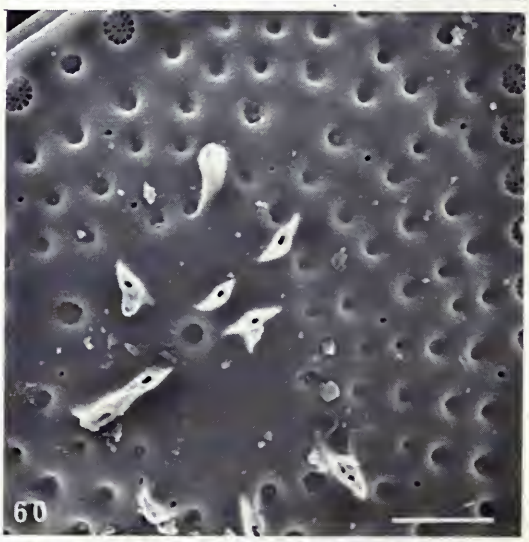

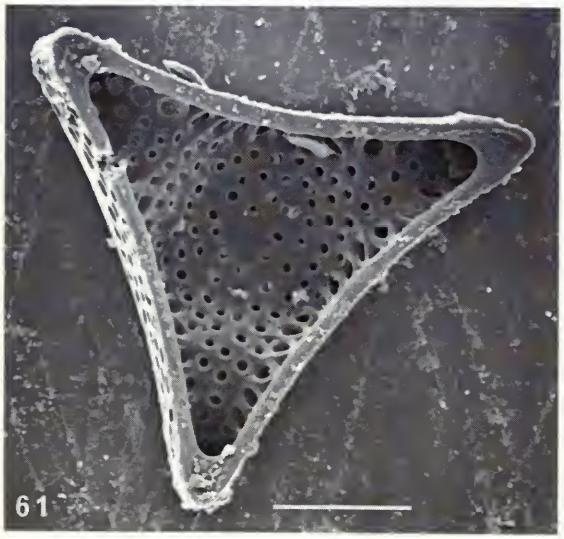

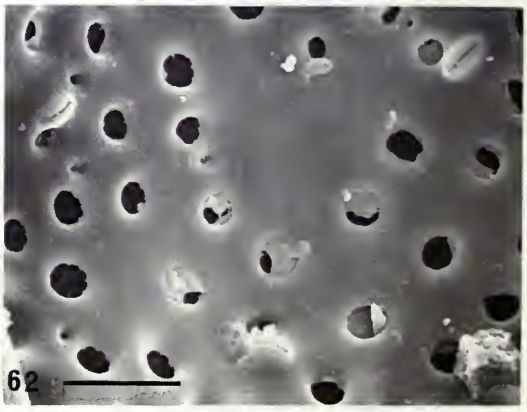

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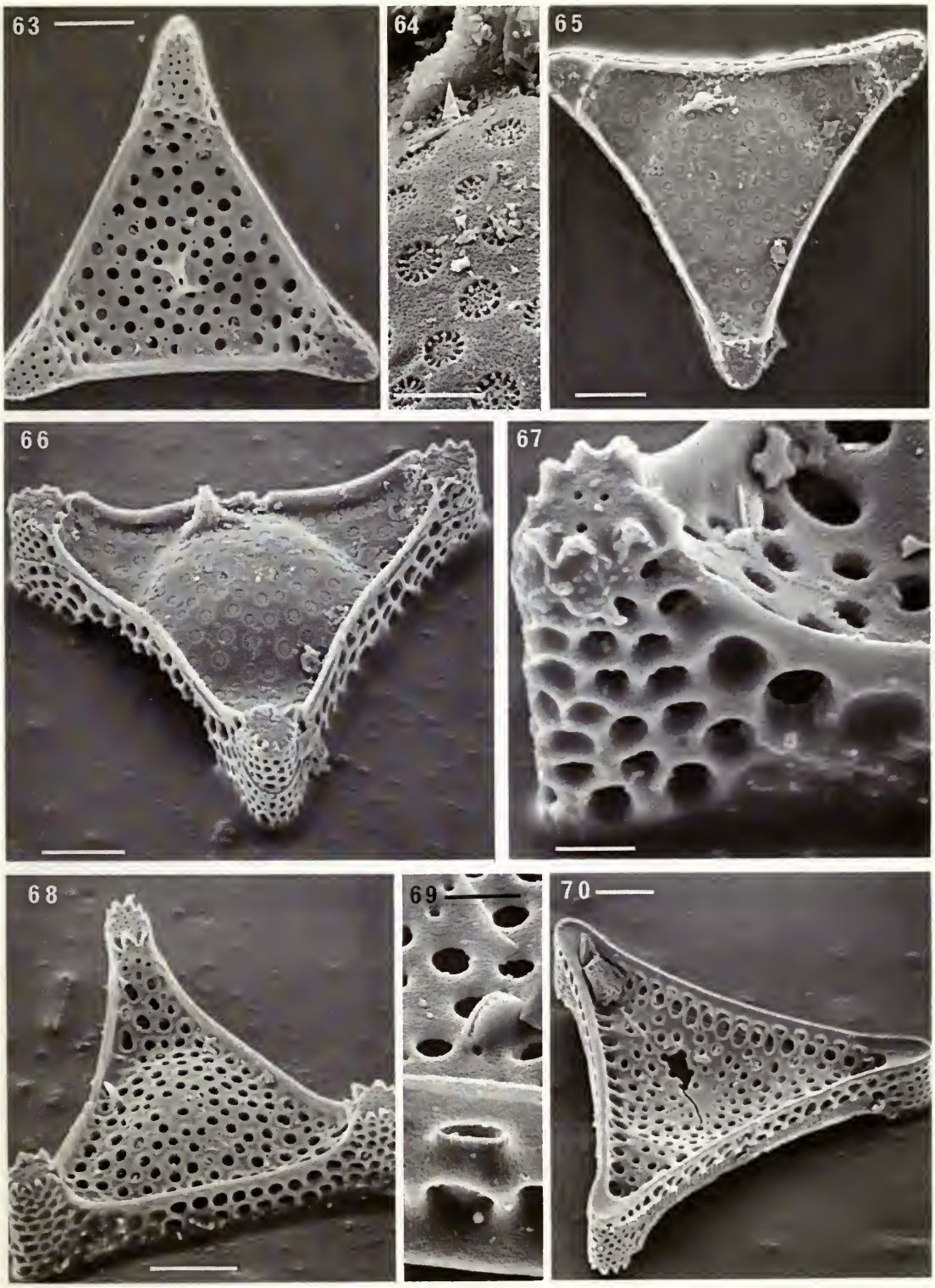

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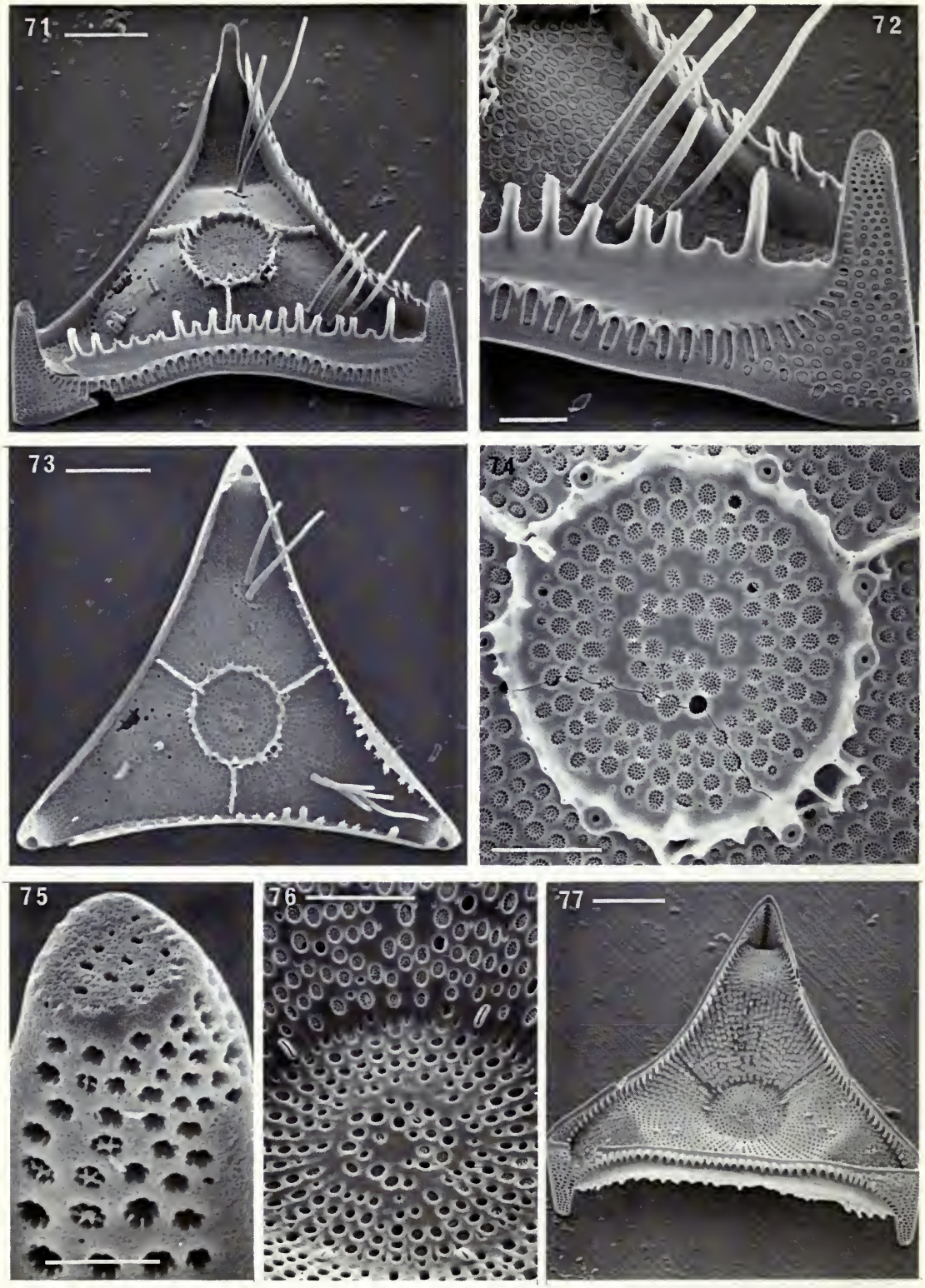

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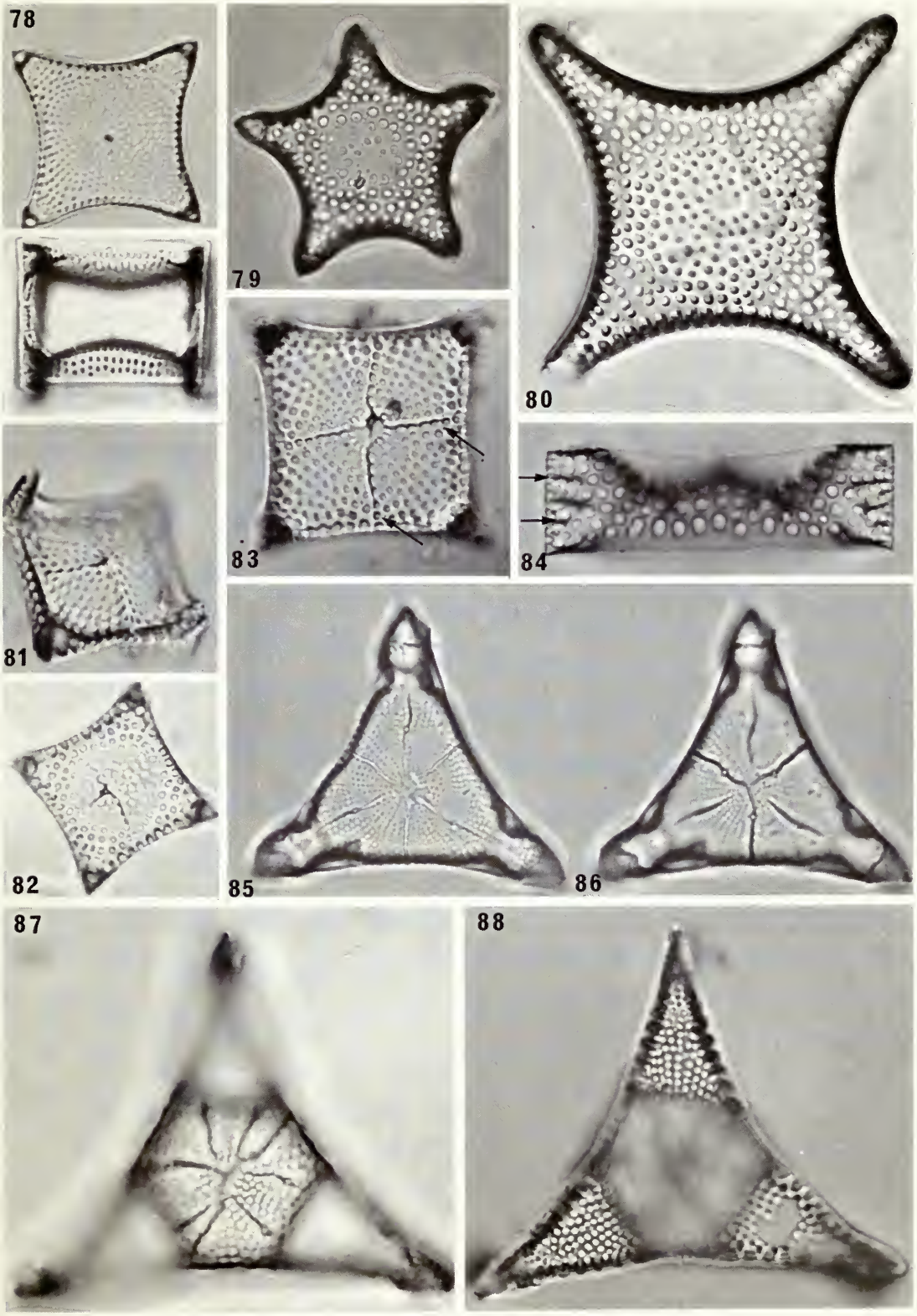

Plate 12

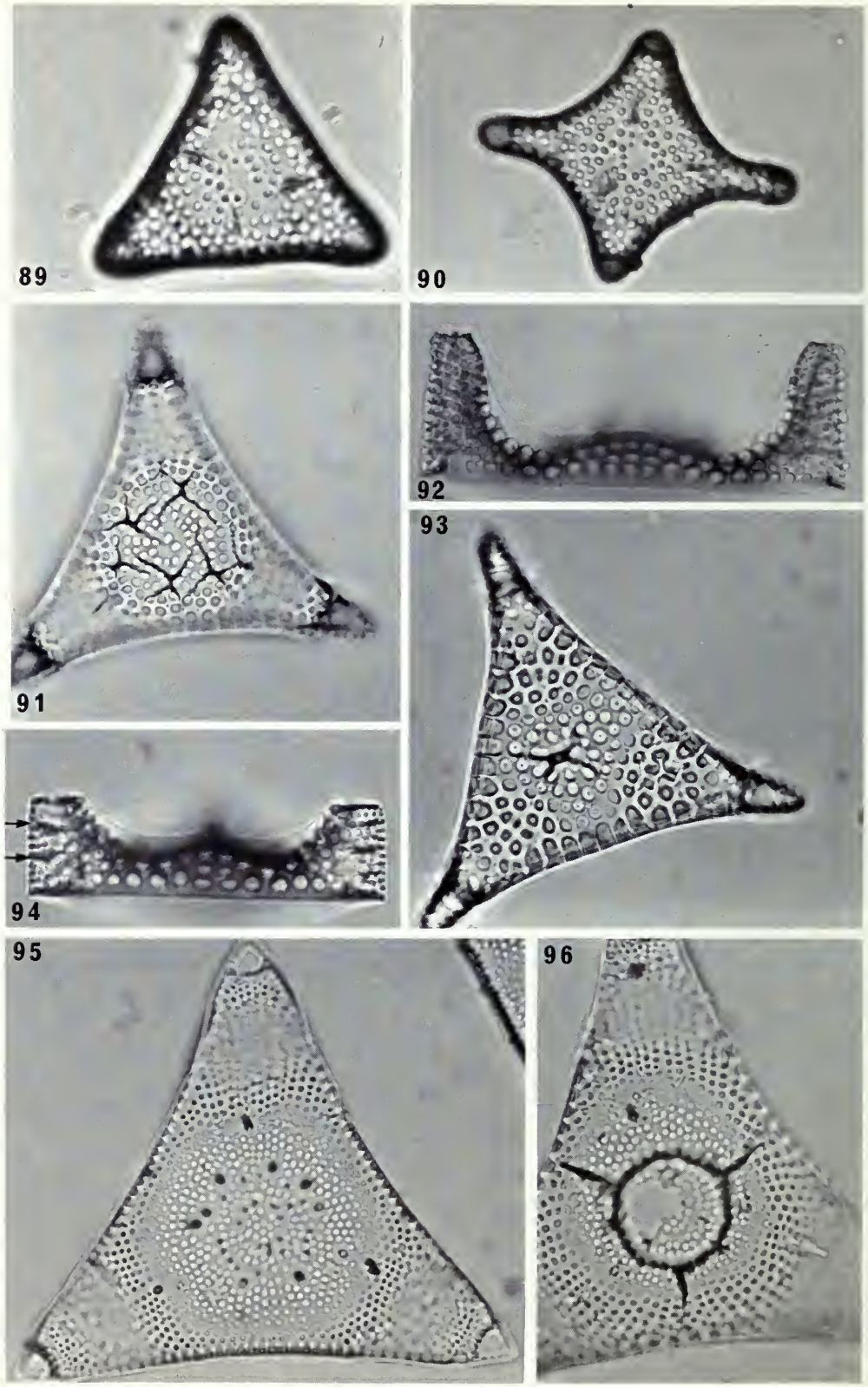

Plate 13

British Museum (Natural History)

MACROLICHENS OF EAST AFRICA

T. D. V. Swinscow and H. Krog

Dr Swinscow was formerly Deputy Editor of the British Medical Journal.
Dr Krog is Professor of Taxonomic Botany at the University of Oslo.

This book is based mainly on collections made in the field by the authors. It covers 77 genera and 629 species. It is the first substantial study of a tropical lichen flora to be undertaken by modern research methods. Thin-layer chromatography has been used throughout, and the great majority of species have been studied by microscopic examination of microtome sections. The nomenclature has been thoroughly revised, and in all cases the basionym is given. The book will be indispensable to students of the lichens of the African continent and valuable to readers interested in lichens throughout the tropics.

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